

The significance of fine-scale climate for plants

Submitted by Owen Greenwood, to the University of Exeter as a thesis for the degree of Masters by Research in Biological Sciences, March 2018.

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Abstract

1. Global climate change will be one of the biggest threats to biodiversity over the course of this century. 21st century biodiversity conservation thus depends much on our ability help species adapt. A better understanding of the importance of fine-scale spatial variation in climatic influence on biodiversity response to climate change is needed to apply management effectively. Current methods utilising coarse-scale variation may not account for the climate a species experiences, leading to inaccurate predictions of species response to climate change.

2. To better understand the importance of climatic influence on biodiversity, this thesis looks at the fine-scale patterns and environmental influences of plant community change in response to climate change, and how these responses can be manipulated through *in situ* management. The first data chapter in this thesis looks at the long-term, fine-scale patterns of a plant community's response to climate change, and the drivers of these. The next data chapter looks at the processes by which microclimate influences the distribution of plants at the fine-scale, focussing on plant species from a range of major biomes. This thesis finishes with a review of the published evidence for whether *in situ* management can be effective in offsetting the adverse impacts of climate change through microclimate manipulation.

3. Chapter 2 looks at long-term, fine-scale changes in plant community composition on the Lizard Peninsula, United Kingdom, since 1900. Using species' indices for temperature, nitrogen and moisture, mean community index values were calculated for 1 km² grid cells over three periods: 1900-1958, 1986-1999 and 2000-2013. The change of each mean index value between these

periods for each grid cell was modelled against spatial variation in a number of environmental variables including distance from the coast, and proxies of water availability and near-ground temperature. The change maps suggest that the majority of cells saw significant increase in January and July temperatures and moisture availability, and significant declines in nitrogen availability. Recorded changes were influenced by distance to the coast, terrestrial warming, topographic wetness, elevation, dominant land cover, and spring solar index.

4. Chapter 3 looks at how habitat variation affected distribution of rare and threatened plant species. Random encounter surveys were carried out between May to September 2013, along public pathways on the Lizard peninsula. Slope, aspect, percentage bare ground cover, soil depth and vegetation height were then measured around individuals. These variables were compared between species with different preferences. This study finds that topography and sward height influence on microclimate affected species distribution. Species with the warmest and coolest temperature associations are both found in the warmest, driest microclimates. These microclimates are predominantly on south-facing, steep slopes with low sward cover.

5. Chapter 4 reviews the available literature to determine the suitability of *in situ* habitat management to manipulate microclimate to promote species persistence. Web of Science was used to search for key terms related to climate change and management, identifying 67 relevant papers for this review. Each management technique identified was then assessed for strength of evidence and risk of failure. This review finds that manipulation of habitat can be used to alter the microclimatic conditions organisms experience to mitigate the effects of climate

change on species as regional climatic conditions became unsuitable. However, many manipulations are not ingrained in conservation practice, and may have negative impacts if applied without consideration.

6. *Synthesis and applications.* Overall, the findings outlined in this thesis suggest that fine-scale environmental variation influences species' response to climate change. If there is a fine-scale influence on species distribution, using coarse-scale SDMs in heterogeneous environments may underestimate species persistence in their current range. Based on our review, *in situ* management is effective at manipulating local environments to offset the effects of climate change. By exploiting this knowledge, conservation managers could manipulate habitat to influence species response to climate change, and more effectively conserve biodiversity.

Acknowledgements

I would like to thank my supervisor Ilya Maclean, as well as Regan Early, for their help, support and patience during my thesis, and Rob Wilson for initially inspiring me to begin my research and his continued support. I would also like to thank Andy Suggitt for his advice and support over the course of my Masters. Thanks to Robin Curtis and Hannah Mossman for their knowledge and input which helped make my fourth chapter as robust and impactful as it has been.

I would also like to thank Regan Early's research group, for keeping me on my scientific toes, and the CLES Teaching Team for keeping me sane. I would like to thank Olivia Lee, Ellie Sargent, Jared Wilson-Aggarwal, Fraser Bell and Roz Evans for their feedback on my writing and general support, as well as Julien Marcetteau for his collaboration on learning the utility of for loops in R.

In addition, I would like to thank my examiners for their comments and feedback, which helped improve this thesis and helped shape any future publications arising from it.

And finally, I would like to thank Jon Blount and the PGR team for their support during my somewhat extended Masters.

Table of Contents

Title Page	1
Abstract	2
Acknowledgements	5
Table of Contents	6
List of Figures	8
List of Accompanying Material	10
Author's Declaration	11
Publications	12
Chapter 1: Introduction	13
Ecological responses to climate change: the importance of scale	13
Patterns of species distribution shifts in response to climate change	16
Influence of microclimate on species distribution	17
Relevance of microclimatic associations for <i>in situ</i> conservation management in response to climate change	19
Chapter 2: Mapping long-term environmental change in response to climate change in a floristically diverse region	21
Summary	21
Key-words	22
Introduction	22
Methods	25
Study system	25
Changes in community indicator values	26
Community indicator prevalence changes	28
Drivers of biodiversity change	28
Results	31
Overall patterns of temporal change in EIVs of plant communities	31
Drivers of biodiversity change	41
Discussion	46
Patterns of change	46
Change drivers	49
Conclusion	58
Chapter 3: The influence of microclimate of species distribution	60
Summary	60
Key-words	61
Introduction	61
Methods	65
Study System	65
Survey Methods	70
Data Analyses	73
Results	74
Temperature Preferences	74
Major biome	76
Vegetation height	77
Discussion	78

Chapter 4: Using <i>in situ</i> management to conserve biodiversity under climate change	86
Summary	86
Key-words	87
Introduction	87
Materials and methods	89
Management to offset the effects of temperature change	90
Management to offset the effects of water availability change	99
Management to offset the effects of sea-level rise	101
General <i>in situ</i> management techniques	105
Conclusions	108
Chapter 5: Conclusion	110
Future directions	110
Conclusion	112
Appendix	113
Chapter 2	113
Figure S2.1	113
Figure S2.2	114
Chapter 3	115
John Wiley and Sons License	115
Chapter 4	121
Appendix S1	121
Appendix S2	126
Appendix S3	133
Table S1	134
Table S2	134
Table S3	136
Bibliography	139

List of Figures

Chapter 2

Figure 1.: Grid cell maps of absolute change, and change significance, of mean January temperature indicator values between periods.

Figure 2.: Grid cell maps of absolute change, and change significance, of mean July temperature indicator values between periods.

Figure 3.: Grid cell maps of absolute change, and change significance, of mean nitrogen indicator values between periods.

Figure 4.: Grid cell maps of absolute change, and change significance, of mean moisture indicator values between periods.

Figure 5.: Histogram of change in proportion of records associated with a given January temperature indicator value between periods two and three.

Figure 6.: Histogram of change in proportion of records associated with a given July temperature indicator value between periods two and three.

Figure 7.: Histogram of change in proportion of records associated with a given moisture indicator value between periods two and three.

Figure 8.: Histogram of change in proportion of records associated with a given nitrogen indicator value between periods two and three.

Table 1.: Table of predictors which best explained changes in community indices between periods two and three.

Chapter 3

Figure 1.: Map of the geological bedrock of the Lizard Peninsula, with survey site locations.

Table 1.: List of coastal grassland species surveyed on the Lizard Peninsula, with their associated temperature preferences, major biome, and number of individuals surveyed for each species.

Figure 2.: Map of species' major biomes, based on biogeographical regions.

Figure 3.: Relationship between microclimatic and macroclimatic temperature associations of selected species on the Lizard Peninsula, Cornwall.

Figure 4.: Relationship between microclimate temperature associations of selected species on the Lizard Peninsula, and the major biome with which they are associated.

Figure 5.: Relationship between the number of occupied 10km cells across the British Isles and the Channel Islands presence and mean sward height of grid cells in which species occurred on the Lizard Peninsula.

Chapter 4

Table 1.: Management responses to climate change.

Table 2.: Ineffective management responses to climate change.

List of Accompanying Material

Chapter 2

Figure S2.1.: Funnel plots of the changes in mean indicator values between periods

Figure S2.2.: Distribution plots of absolute changes across 1km² cells for indicator value changes between periods.

Chapter 3

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Chapter 4

Appendix S1.: Details of systematic literature review

Appendix S2.: Additional information and references associated with Table 1

Appendix S3.: Additional information and references associated with Table 2

Table S1.: Scheme for cross-tabulating scores associated with the magnitude of a response and the confidence in the response, to derive overall scores of the strength of evidence associated with each study.

Table S2.: Scheme for scoring the strength of evidence for management techniques tested in multiple studies.

Table S3.: Management responses to climate change, with associated effects on the environment and on wildlife.

Author's Declaration

All chapters, except chapter 4, were written by Owen Greenwood, with comments provided by Dr. Ilya Maclean and Dr. Regan Early. Chapter 4 was written with the assistance of the co-authors on this publication, with Owen Greenwood writing the Abstract, Introduction, with revision, Materials and Methods, and all tables and supporting information, including appendices.

Data collection and analysis was performed by Owen Greenwood. Various academics, botanical specialists and members of the public contributed to the long-term ERICA database used in Chapter 2. Dr. Ilya Maclean provided the means to calculate the Solar Index values used in Chapter 3. Where any other data was derived from sources other than data collection, this is outlined in the relevant Methods section.

Publications

At time of printing **Chapter 4** has been published in *Journal of Applied Ecology*, exactly as it appears here, except for minor Supplementary Material edits.

Using *in situ* management to conserve biodiversity under climate change

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Chapter 1: Introduction

Ecological responses to climate change: the importance of scale

Climate change is recognised as one of this century's major threats to global biodiversity, alongside habitat loss, pollution, and invasive species (Thomas *et al.* 2004; Wake & Vredenburg 2008; Clavero, Benejam & Seglar 2009; Maclean & Wilson 2011; Trathan *et al.* 2015). As a result of these anthropogenic pressures, global extinction rates over the past century were around 100 times higher than historic rates, and are expected to accelerate further (Millenium Ecosystem Assessment 2005). Over the last 40 years, an increasing number of studies have endeavoured to predict ecological responses to climate change (Beaumont *et al.* 2011; Dawson *et al.* 2011; McMahon *et al.* 2011). Many ecological responses are expected due to species distribution shifts as species attempt to continue to occupy suitable climatic conditions under anthropogenic climate change. Most studies have predicted species distribution shifts using species distribution models (SDMs) based on macroclimatic changes at a scale of tens to hundreds of kilometres. This is at odds with the scale at which species experience climate (Potter, Woods & Pincebourde 2013). Predictions for biodiversity response to climate change are often made using SDMs, which have shown themselves be powerful predictive tools (Phillips, Dudík & Schapire 2004; Guisan & Thuiller 2005). SDMs combine species distribution data and species environmental associations to current environmental conditions to predict distribution changes under predicted future environmental conditions over time. Recently, studies have investigated the effect of microclimatic variation on species distribution changes and its potential importance under future climate change (Suggitt *et al.* 2012; De Frenne *et al.* 2013; Scheffers *et al.* 2014a). These studies found that

microclimate can affect species distribution in areas with heterogeneous environments. This suggests that SDMs which make use of fine-scale data may provide more accurate predictions for species distribution shifts in heterogeneous environments. Consequently, they may identify holdouts within areas of unsuitable macroclimatic conditions. Accurate ecological response predictions are important because they provide conservation managers with useful information to help offset the adverse effects of climate change on biodiversity.

Predictive studies of climate–organism interactions usually rely on coarse-resolution climate variables measured over tens to hundreds of kilometres, whereas the conditions experienced by many organisms vary over scales from millimetres to metres (Potter, Woods & Pincebourde 2013). Coarse-scale SDMs bridge this spatial mismatch by assuming that macroclimatic conditions of an area can be used to accurately predict ecological responses (Bennie *et al.* 2014). However, the implications of this spatial mismatch and the conditions under which coarse-resolution climate data fails to accurately predict responses to climate change for coarse-scale SDMs are not fully understood. For example, Randin *et al.* (2009) found that SDMs using coarse-resolution data predicted that as few as 13 of the 78 mountain plant species (16.6%) studied in the Swiss Alps would retain suitable habitat during the 21st century. On the other hand, SDMs using fine-resolution data predicted that potentially all 78 species (100%) could retain suitable habitat. However, in a similar environment Trivedi *et al.* (2008) found the opposite trend. Their analysis predicted distribution of ten montane species at the coarse-scale had a 62% match to current distributions, with only a 26% match at the fine-scale. This highlights that many issues around fine-scale and coarse-scale models are not well understood.

The likely cause for the disparity between coarse and fine-scale model predictions is the inability of coarse-scale models to capture topographic and vegetative cover heterogeneity (Luoto & Heikkinen 2008). Without information on the topographic and vegetative influence on climatic conditions, it is very difficult to predict the effects of climate change on available microclimates. In heterogeneous environments fine-scale SDMs could be used to predict areas in which microclimatic conditions may differ from broad scale average macroclimatic conditions. This could lead to identification of suitable microclimatic holdout locations in an area defined as macroclimatically (i.e. at the coarse-scale) unsuitable for a given species. I define a holdout here as a population which persists in a suitable microclimate for a limited time period within an area with unsuitable macroclimatic conditions (Hannah *et al.* 2014). Holdouts differ from microrefugia as holdouts only enable persistence for a limited time under climate change, whereas microrefugia are areas in which they persist interminably. Many species take advantage of holdouts to persist within areas with unsuitable macroclimatic conditions. For example, species are able to occupy areas with more suitable warmer (Lawson *et al.* 2012) microclimates than expected from macroclimatic averages. Fine-scale variation in moisture availability has similarly been shown to influence species habitat association, allowing species to live in areas with greater water availability (Carroll *et al.* 2011) than expected from the regional macroclimate averages. Consequently, predictions of future species distributions under differing climatic conditions made using coarse-scale models may provide an inaccurate picture of species distribution changes. With the threat of climate change, conservation planning relies on accurate predictions of

changes in species distributions to determine where and how conservation managers need to respond.

Patterns of species distribution shifts in response to climate change

Given that many species experience climate at the fine-scale, I argue that species distribution response to climate change is influenced by fine-scale climatic variation. Fine-scale climatic variation has been shown to influence species distribution. If the influence of fine-scale environmental variation on species response to climate change is understood, predictions of species distribution changes could be made with greater accuracy at a fine-resolution. With more accurate predictions of species distribution changes, conservation efforts could be focused on regions where management would be most effective for mitigating biodiversity loss resulting from climate change.

Global anthropogenic climate change has been occurring for over a century. Despite this, studies examining the long-term, fine-scale community responses to climate change over a similar period are lacking. Lack of long-term datasets of species records at the fine-scale is one of the main reasons for this. In particular, determining the influence of climate change on species distributions becomes problematic when (i) community responses only occur after a certain threshold of climatic change (Shi *et al.* 2015), or (ii) when long-term community responses can be masked by short-term variability (Lawson *et al.* 2015).

In chapter 2 I identify the influence of climate change on fine-scale plant community change over the long term using plant records from the Cornwall focused database ERICA (French 2010). The ERICA database is collated from

professional and amateur sources. I use the long-term, fine-scale dataset available for the Lizard Peninsula, Cornwall, which spans from the 1800s to the present (Johns 1848; Maclean *et al.* 2015). ERICA contains over 190,000 plant records for the Lizard Peninsula to at least 1 km resolution. This allows study of community change over a similar period to that of anthropogenic climate change (>100 years). In addition, I investigate the change drivers responsible for the fine-scale variation in community response to climate change seen. Change drivers included topographic wetness, dominant land cover type, distance from the coast, mean terrestrial warming, mean spring, summer and autumn solar index, elevation, and accumulated flow. Most fine-scale studies are short, meaning that they can't evaluate biodiversity responses to the several decades of climate change we have now seen. This is one of the longest running records of fine-scale responses to climate change known. By using a long-term, fine-scale database such as ERICA, it was possible to see fine-scale plant community response to climate change, and the role each of the change drivers played in community response variation.

Influence of microclimate on species distribution

There seems to be no consensus in the literature of the scale by which it is best to predict changes in species distributions as a result of climate change. There is an argument that coarse-scale SDMs bridge the mismatch between the scale at which climate affects species distributions and the scale at which distributions are modelled, albeit implicitly, through 'mean field approximation'. Mean field approximation is where grid cell climate variable averages are statistically meaningful predictors of species persistence likelihood within that grid cell (Bennie *et al.* 2014). Others argue that climate is relatively unimportant at the fine

scale, when compared to factors such as biotic interactions (Pearson & Dawson 2003), and so coarse-scale models would make accurate predictions for distribution changes .

In chapter 3 I investigate the influence of topographic variation on microclimate and the consequent impact on species distribution. From this I aim to determine the suitability of fine-scale resolution data in SDMs to provide accurate predictions of biodiversity response to climate change. Specifically, I look at the influence of solar insolation and vegetation cover on species distribution of coastal grassland and heathland plants of the Lizard Peninsula, UK. I measured slope, aspect, soil depth, and sward height in a 0.5m² quadrat centred on target species specimens in the field. I took field measurements for species from a range of major biomes to assess the relationship between a variety of species' macroclimatic and microclimatic associations. To provide a proxy of microclimate in each quadrat, I calculated each quadrat's mean solar insolation between 1st of April and 1st of August, based on solar zenith and azimuth. The solar zenith and azimuth are functions of latitude Julian day and were derived using methods detailed in Hofierka & Šúri (2002) and Bennie *et al.* (2008). Solar insolation plays an important role in determining near-surface temperatures, evaporative demand, and soil moisture of a site at the fine scale (Bennie *et al.* 2008; Suggitt *et al.* 2011; Maclean *et al.* 2017). I compared the mean solar insolation and sward height of areas species occupied with the species' recorded macroclimatic associations and broad scale distributions. I found that species distribution can be shaped by fine-scale climatic variations, and so may not be influenced by coarse-scale climatic conditions as predicted.

Relevance of microclimatic associations for *in situ* conservation management in response to climate change

Ex situ conservation measures, such as species translocations (Thomas 2011) and the redesign of protected area networks (Araújo *et al.* 2011) are often presented as options for managing distribution shifts of species at risk from climate change. While they can be applied successfully (Molles *et al.* 2008; Gleason *et al.* 2010), they are often unfeasible. For example, species can be isolated within surrounding hostile environments as a result of anthropogenic habitat manipulation (Mantyka-Pringle, Martin & Rhodes 2012). In other situations, species range shifts may not be rapid enough to keep pace with anthropogenic climate change (Menéndez *et al.* 2006). In both these circumstances, redesign of protected area networks is not very effective. Additionally, translocations may be limited by financial cost (Beringer *et al.* 2002) or availability of suitable space (Liu *et al.* 2001; McRae *et al.* 2012). Thus, looking at *in situ* management options may be an effective way to conserve immobile or isolated species in the face of climate change.

In chapter 4 we look at *in situ* options for habitat management, and the benefits and risks associated with each method for species conservation in the face of climate change. We review the growing available literature to determine how *in situ* management could be used to manipulate climatic conditions to species' benefit. Within the literature, there is a lack of clear guidance to support how such management can be achieved, or how successful or risky a given technique is. There are species which rely on human habitat manipulation to persist in their current distribution (Luoto, Pykälä & Kuussaari 2003), as well as species which shift their local distribution in response to climatic variation (Suggitt *et al.* 2012).

These situations suggest that habitat manipulation can be used to buffer species response to adverse effects of climate change. Potential habitat management techniques were identified by searching Web of Science using terms related to climate change and management. Also included were any additional studies already known to the authors. This resulted in 62 relevant papers being identified. These papers were assessed for strength of evidence and risk of failure for unique techniques identified. While many techniques had at least moderate risk of failure, they also had moderate to high strength of evidence for success when applied with care. The strength of evidence suggests that there are *in situ* management techniques which can be utilised to manipulate climate change for the benefit of species persistence, and thus conservation of biodiversity. Chapter 4 provides conservation managers with a toolbox of known *in situ* management techniques to conserve biodiversity in the face of global climate change, and the benefits and risks associated with them.

Chapter 2: Mapping long-term environmental change in response to climate change in a floristically diverse region

Summary

1. It is well documented that plant and animal species are responding to environmental change. However, few opportunities present themselves to study the long-term effects, particularly for multiple species at fine spatial scales.
2. Here, I examine fine-scale changes in plant community composition on the Lizard Peninsula, United Kingdom over 113 years of anthropogenic change. I use temperature indices and Ellenberg Indicator Values (EIVs) for nitrogen and moisture and relate these to changes in environmental conditions to establish the likely causes of change. I identify areas least susceptible to change and offer insight into why. Mean community indices were calculated for each 1 km grid cell over three periods: 1900 to 1985, 1986 to 1999 and 2000-2013 and the change between periods in each grid cell was modelled against spatial variation in land cover, distance from sea, proxies of water availability and near-ground temperature, as well as fine-scale temperature change.
3. Significant changes in plant community composition have occurred between 1900 and 2013. Community January and July temperature and moisture indices tended to decrease between during the 20th century but tended to increase in the early 21st century. Community nitrogen indices showed the opposite pattern. Based on mixed regression models,

community changes were influenced by changes in temperature, moisture availability, and nitrogen. Changes in temperature, moisture availability, and nitrogen mean indicator values varied due to spatial variation in topography, dominant land use, and coastal proximity, as well as temporal variation in warming.

4. *Synthesis and applications.* My results suggest changes in plant community composition have occurred on the Lizard in line with changes in climate and land use. To my knowledge, this is among the first studies to document long-term (>100 year) plant community responses to anthropogenic change at the fine-scale. My findings provide insight into the drivers of spatial variation in responses to change and facilitate the identification of resilient habitats. Such areas may serve as vital safe havens for biodiversity under projected anthropogenic warming.

Key-words: biodiversity conservation, biological records, environmental change, global warming, microclimate, plant community

Introduction

Global extinction rates over the last century are in the region of 100 times higher than historical background rates (Millenium Ecosystem Assessment 2005). These losses are largely attributable to rapid changes in environmental conditions brought about by human activities (Foley *et al.* 2005). Shifts in global development have resulted in major threats to biodiversity principally from climate change, habitat loss and fragmentation, pollution and the spread of invasive species (Thomas *et al.* 2004; Wake & Vredenburg 2008; Clavero, Benejam &

Seglar 2009; Trathan *et al.* 2015). These drivers often act in combination to create what Barnosky *et al.* (2011) describe as a 'perfect storm', whereby multiple stressors act concurrently to induce high rates of extinction. The simultaneous nature of these stressors and the varying degrees to which they matter at local scales makes it difficult for environmental managers to know how to respond. To manage habitats effectively, one needs to distinguish between the effects of different drivers of biodiversity loss. However, obtaining such knowledge is made challenging by the paucity of long-term records that allow the individual effects of multiple drivers to be fully understood (Tylianakis *et al.* 2008; Greenwood *et al.* 2016).

While major anthropogenic environmental change has been occurring for over a century (Foley *et al.* 2005), there are very few studies that examine the ecological effects of these changes over a comparable period, particularly for multiple species at the fine spatial scale relevant to management. The disparity between the temporal periods over which changes have occurred and those at which studies are conducted, makes it more difficult to partition the effects of individual stressors. The influence of climate change on biodiversity can either be compounded (Forister *et al.* 2010; Stevens *et al.* 2015) or offset (Warren *et al.* 2001) by habitat change. This illustrates the importance of understanding the environmental response to climate and habitat changes over a similar time-span (Stenseth *et al.* 2002). It is necessary to document the effects of long-term changes over comparably long periods, both because some changes only result in a response when they reach a certain threshold (Scheffer *et al.* 2001; Shi *et al.* 2015) and because species' responses to long-term environmental changes can be masked by responses to short-term variability (Lawson *et al.* 2015).

In this study, I map and examine long-term changes in plant communities in one of the most data rich regions of the planet. The Lizard Peninsula, in Cornwall, UK has an extensive history of botanical interest dating back to the 17th century. Beginning with observations made by John Ray in 1667, botanical interest on the Lizard has been maintained ever since (Johns 1848; Coombe & Frost 1956; Malloch 1971; Pearman 2017), resulting in an unrivalled long-term dataset of plant records. Kosanic *et al.* (2015) identified the loss of 17 species from different sites in Cornwall comparing pre- and post-1900 plant records. I wanted to elucidate the community changes in an area of botanical interest within Cornwall which have occurred over a similar period. To assess the drivers of community change, I derive environmental indicators for plant communities and document changes of these in 1 km grid cells. Firstly, I use species temperature indices to assess how plant communities may have responded to increasing temperatures. Secondly, I use species Ellenberg Indicator Values (EIVs) for nitrogen and moisture (Ellenberg *et al.* 1991; Hill, Preston & Roy 2004) to assess how plant communities may have responded to changes in nitrogen deposition, agricultural run-off and water availability. These data allow me to map the ecological response to climate and habitat change on the Lizard Peninsula over a comparable period to that over which major changes have occurred. I also look at the effect of the drivers of change on the extent of climate change's impact on species distribution. These drivers included spatial environmental predictors such as dominant land cover and proxies of fine-scale spatial variation in temperature and water, as well as a temporal predictor, namely fine-scale variation in warming.

Methods

Study system

This study investigated floristic community changes on the Lizard Peninsula Cornwall, United Kingdom (UK; 50.143°N, 5.124°W). Due to the serpentine bedrock, in conjunction with its warm, wet winters and mild summers, the Lizard is a unique environment in England, and hosts many threatened plant species endemic to the United Kingdom (Ratcliffe 1977; Byfield 1992).

The Lizard's rich botanical history has resulted in an extensive floristic dataset of 197,574 records (for the region shown in Fig. 1), which is held by the Environmental Records In Cornwall Automated (ERICA) database (French 2010). Each record is assigned an observer, a date and geographic location to varying degrees of precision. Though comprehensive, the data are not systematically recorded, and represent sightings voluntarily submitted by professional and citizen scientists. However, all records are also verified by experienced botanists. Most records since 1900 have been georeferenced to a precision of 1 km or less, which allows for relatively high-resolution mapping of environmental changes based on variation in the environmental associations of the plant community. I use this dataset to indicate environmental changes spanning the past century and create one of the longest-term fine-scale analyses of environmental change indicators for any region of the planet. Records were split into three periods: 1900 to 1985 (period one), 1986 to 1999 (period two) and 2000 to 2013 (period three). The rate at which species records have been obtained has accelerated in recent years. The time-span between periods was selected to make periods two and three a comparable length while limiting disparity in number of records in each. There were too few records prior to 1985 to sub-divide in to more periods and still

provide adequate coverage of cells across the Lizard peninsula at a 1 km resolution.

Changes in community indicator values

An Ellenberg Indicator Value (EIV) is a value assigned to plant species based on ordinal classification of the position of their realized ecological niche along an environmental gradient. This provides us with a relative value to be able to analyse community change in relation to comparative species values. A species' niche is in part determined by its tolerance range to environmental drivers, such as moisture or nitrogen levels. An EIV is set on an arbitrary scale for each driver, defined by a plant's associated environment types, such as submerged soil (a 12 on the Moisture scale) or infertile soils (a 1 on the Nitrogen scale). EIVs for the British Isles were based on previous work by Ellenberg *et al.* (1991) and derived from existing datasets and field surveys (Hill, Preston & Roy 2004). I used Ellenberg indicator values for moisture and nitrogen. While indicator values for temperature were developed by Ellenberg (1991), their application in oceanic climates is problematic (Hill, Preston & Roy 2004). In consequence, temperature community indicator values were based on macroclimatic temperature associations provided by Hill, Preston and Roy (2004), which represent the mean January and July temperatures of the 10-km squares in which each species occurs in Britain, Ireland and the Channel Islands.

To map indicators of environmental change across the study region, plant records were grouped by period and 1 km² grid cell. The means of each of the four indicator values for species in each grid cell, hereafter referred to as community indices, were calculated for each period. Absolute changes in mean community

index values were calculated for cells between successive periods, one and two (1900-1985, 1986-1999), and two and three (1986-1999, 2000-2013) and mapped across the study area. Cells with only one species in both the periods being compared were excluded. Additionally, funnel plots of the relationship between the number of records and change in mean index values in each grid cell were used to rule out the possibility that changes could be attributed to observer effort, whereby grid cells with low observer effort exhibit greater variance and therefore have arbitrary mean index values. Based on the funnel plot centrality and symmetry, cells that did not have sufficient records were excluded to avoid bias, as these cells were more likely to have extreme mean index values and so skew observed change over time (Fig. S2.1). Between periods one and two, the minimum of records per cell required to avoid bias was four for January temperature index values and one for July temperature and nitrogen index values, and 55 for moisture index values. Between periods two and three, the minimum of records per cell required to avoid observer bias was nine for January temperature index values, 11 for July temperature and nitrogen index values, and one for moisture index values. After filtering the data in this way, there were 190,179 records georeferenced to a precision of at least one km and from cells with more than a single species and valid total record number, of which 29,580 were in period one, 67,089 in period two, and 93,510 in period three. Changes in mean index values between each period in each grid cell were quantified and assessed using a t-test separately in each grid cell to determine change significance.

Community indicator prevalence changes

To assess whether decreases or increases in the prevalence of species with a given indicator value that drove overall changes, cells were partitioned into those in which mean community indices had increased and those which had decreased, and the changes in the proportion of records associated with each indicator value in increasing cells ($\Delta_{p\uparrow}$) and decreasing cells ($\Delta_{p\downarrow}$), was determined as follows:

$$\Delta_{p\uparrow} = p_{i\uparrow 3} - p_{i\uparrow 2}$$

$$\Delta_{p\downarrow} = p_{i\downarrow 3} - p_{i\downarrow 2}$$

where $p_{i\uparrow}$ is the total proportion of records associated with each indicator value i in increases cells in either period two or three and $p_{i\downarrow}$ is the proportion of records associated with each indicator value in decreasing cells. Here, positive values indicate that the proportion of records associated with a given indicator value increased between periods two and three. Bar plots of proportional change for each community indicator were made.

Drivers of biodiversity change

To identify drivers of plant community changes, absolute change in community index values between periods in each grid cell were modelled against the following predictors using linear regression: topographic wetness (see below), dominant land cover type, distance from the coast (log base 10 transformed), mean terrestrial warming, mean spring, summer and autumn solar index (see below), elevation, and accumulated flow. As period one had a relatively low number of fine-resolution records, it was excluded from these analyses.

Topographic wetness (*Topidx*) was calculated using the method described in Beven & Kirkby (1979), as follows:

$$Topidx = \log_e \left(\frac{a}{\tan b} \right)$$

where *a* is accumulated flow, and *b* is the slope. Both were calculated using ArcGIS 10.2 (ESRI 2014) from a five-metre resolution digital elevation model (DEM) obtained from Bluesky (Bluesky International Ltd. 2014) coarsened to 100m using bilinear interpolation to match the resolution of modelled terrestrial warming data. Land cover was derived from the Centre for Ecology and Hydrology's 2007 Land Cover Map (Morton *et al.* 2011). In this dataset, land cover is classed in to 26 categories of habitats, including grassland types, and land use types, such as arable or improved grassland. Mean terrestrial warming data were obtained from Maclean *et al.* (2017) for the period 1977 to 2014. In this study, five groups of factors were considered to influence local temperatures, namely coastal influences, net radiation, elevation, latent heat exchange and cold air drainage into valley bottoms. Their effects on temperature were modelled at hourly intervals at 100m resolution for the period 1977-2014. Rates of warming were calculated using linear regression of hourly temperatures in each grid cell.

Solar indices were calculated using the mean proportion of potential direct irradiance intercepted by an inclined surface for every hour between December and February (winter), March to May (spring), June to August (summer) and September to November (autumn). The proportion of potential direct irradiance

intercepted by the surface for a given solar zenith and azimuth (hereafter referred to as insolation) was calculated as follows:

$$Ri = \cos S \cos Z + \sin \beta \sin Z \cos(\Omega_s - \Omega)$$

where Ri is the proportion of potential direct irradiance intercepted by the slope, S is the angle of the slope, Z is the solar zenith, Ω_s is the solar azimuth and Ω is the slope aspect. The solar zenith and azimuth are functions of latitude Julian day and were derived using methods detailed in Hofierka & Šúri (2002) and Bennie *et al.* (2008). All derived environmental data were coarsened from their original resolution to 1 km resolution by computing mean values within each 1 km grid cell.

Changes in temperature index values and Ellenberg indicator values as a result of changes in community prevalence were modelled as a function of the drivers of biodiversity change listed above using General Linear models, with Gaussian error structures and identity link functions. The MuMIn package for R (Barton 2016; R Core Team 2016) was used to perform a model dredge to identify the suite of predictors that best explained changes in temperature and Ellenberg indicator value indices between periods two and three. A Monte Carlo procedure was then used to account for the fact that indicator values in each grid cell have an associated uncertainty, whereby indicator value change data points were randomly generated from normal distributions with the same mean and variance as the data from each individual grid cell. The analyses were repeated 10,000 times, and the proportion of times in which coefficient value differences were either greater or less than zero (depending on in the hypothesised direction of

the effect) were used to determine significance. The Monte Carlo procedure hence provides a one-tailed significance for each fixed effect included in the model once the suite of predictors had been identified.

Results

Overall patterns of temporal change in EIVs of plant communities

Between both sets of periods, cells with sufficient records for inclusion were widely distributed across the study region (Fig. 1).

Between periods one and two, mean January temperature community index values significantly decreased in 85.1% of cells (Overall mean change: -0.209 ± 0.282 , Fig. 1a,b), for July temperature in 77.9% (Overall mean change: -0.197 ± 0.302 , Fig. 2a,b), and for moisture in 85.8% of cells (Overall mean change: -0.334 ± 0.317 ; Fig. 3a,b). Mean nitrogen community index values significantly increased in 76.1% of cells (Overall mean change: 0.63 ± 0.918 ; Fig. 4a,b).

Between periods two and three, mean January temperature community index values significantly increased in 80.7% of cells (Overall mean change: 0.043 ± 0.084 , Fig. 1c,d), and for July temperature in 78.7% of cells (Overall mean change: 0.052 ± 0.077 , Fig. 2c,d), with decreases mostly occurring inland for both. Mean moisture community index values significantly increased in 69.2% of cells (Overall mean change: 0.138 ± 0.337 ; Fig. 3c,d), particularly close to coastal areas, with cells showing decreases in the west. Mean nitrogen community index values significantly decreased in 65.4% of cells (Mean overall change: -0.156 ± 0.387 ; Fig. 4c,d).

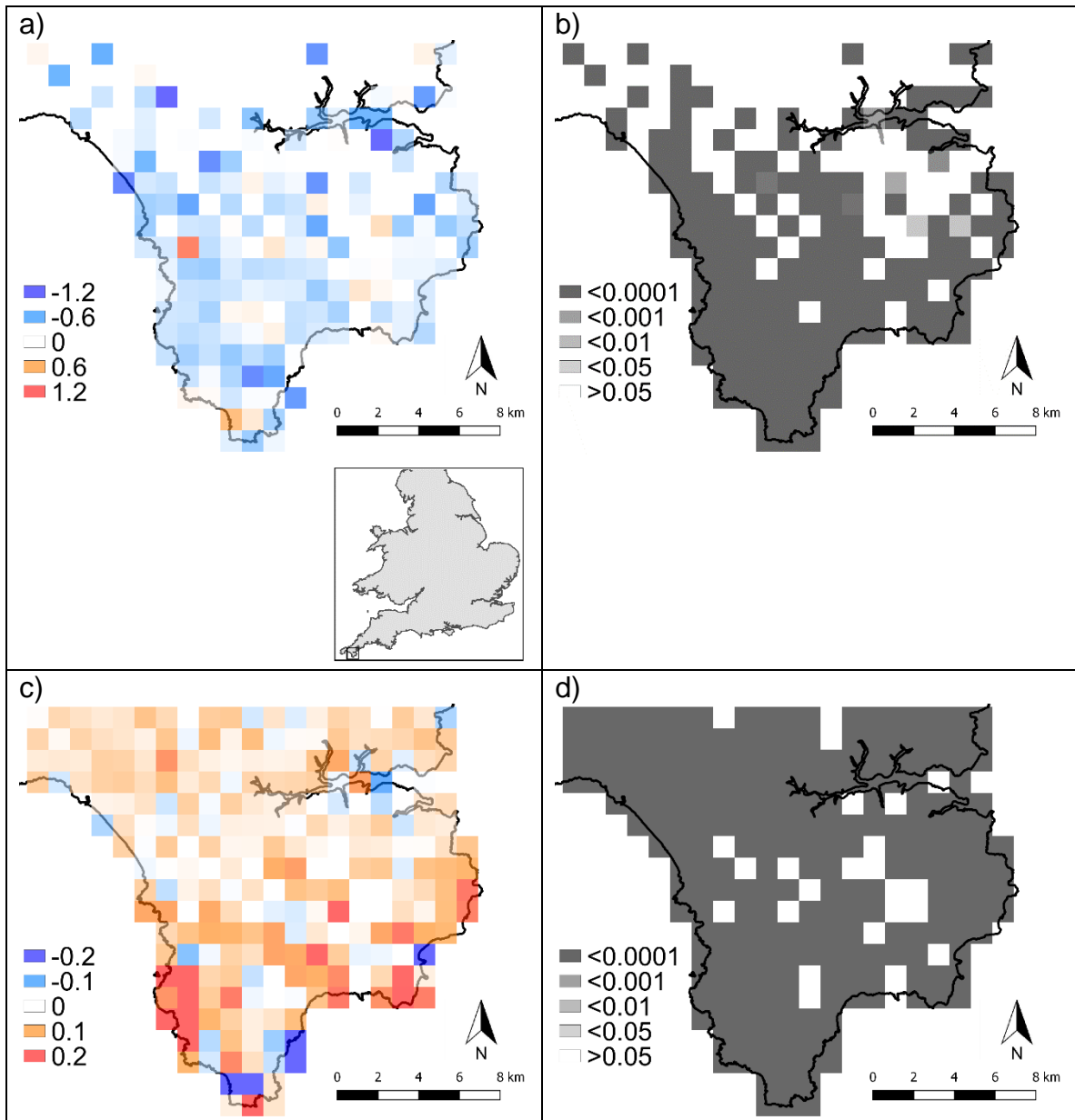


Figure 1. Changes in the January temperature index values of each grid cell (a,c), and significance of change (b,d), between successive periods (1900-1985 and 1986-2000) and (1986-2000 and 2000-2013). Frequency histograms of cell changes between periods are provided in Figure S2.2. An increase in January temperature index values indicates an increase in plants associated with higher January temperatures in the later period.

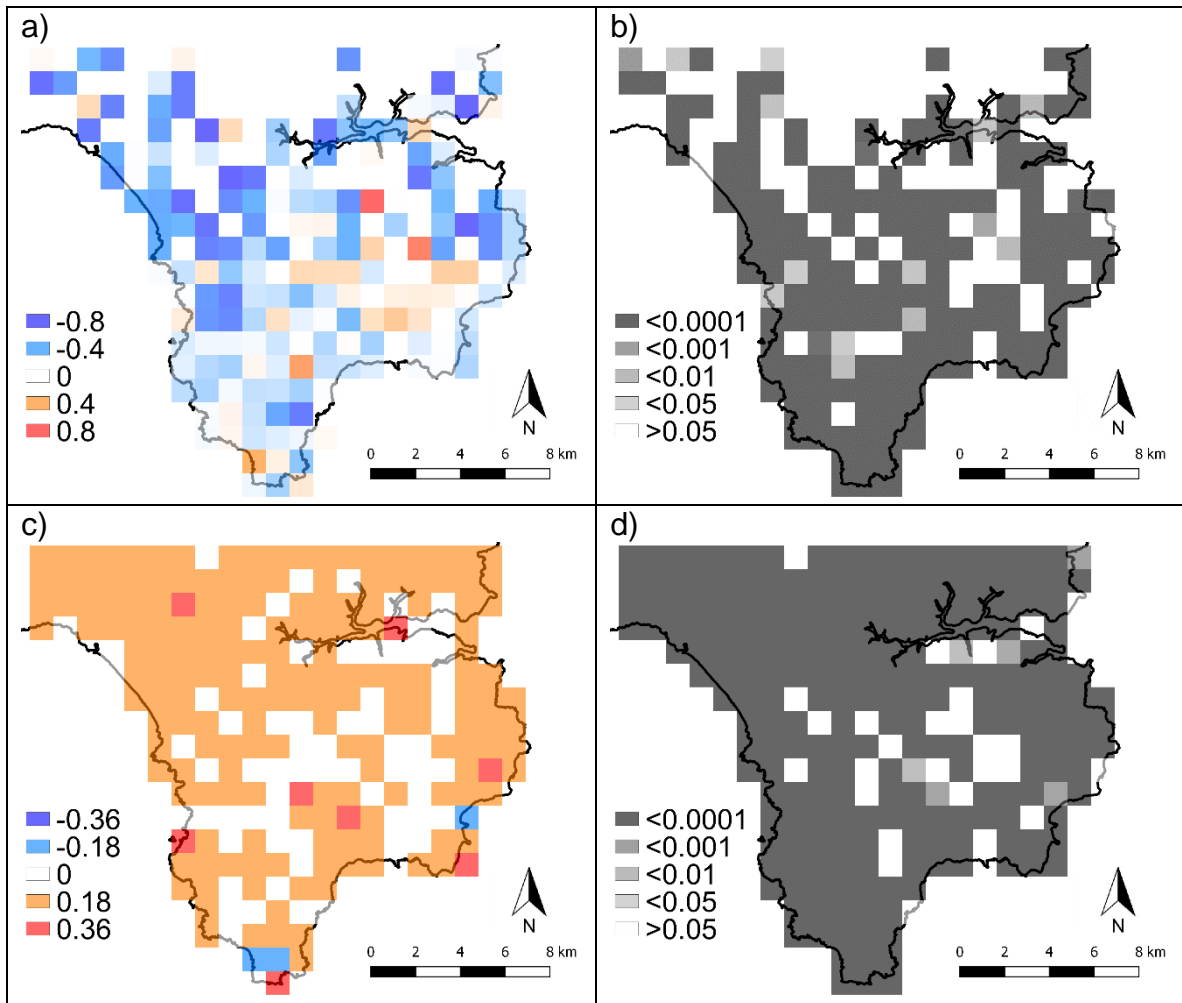


Figure 2. Changes in the July temperature index values of each grid cell (a,c), and significance of change (b,d), between successive periods (1900-1985 and 1986-2000) and (1986-2000 and 2000-2013). Frequency histograms of cell changes between periods are provided in Figure S2.2. An increase in July temperature index values indicates an increase in plants with associated with July temperatures in the later period.

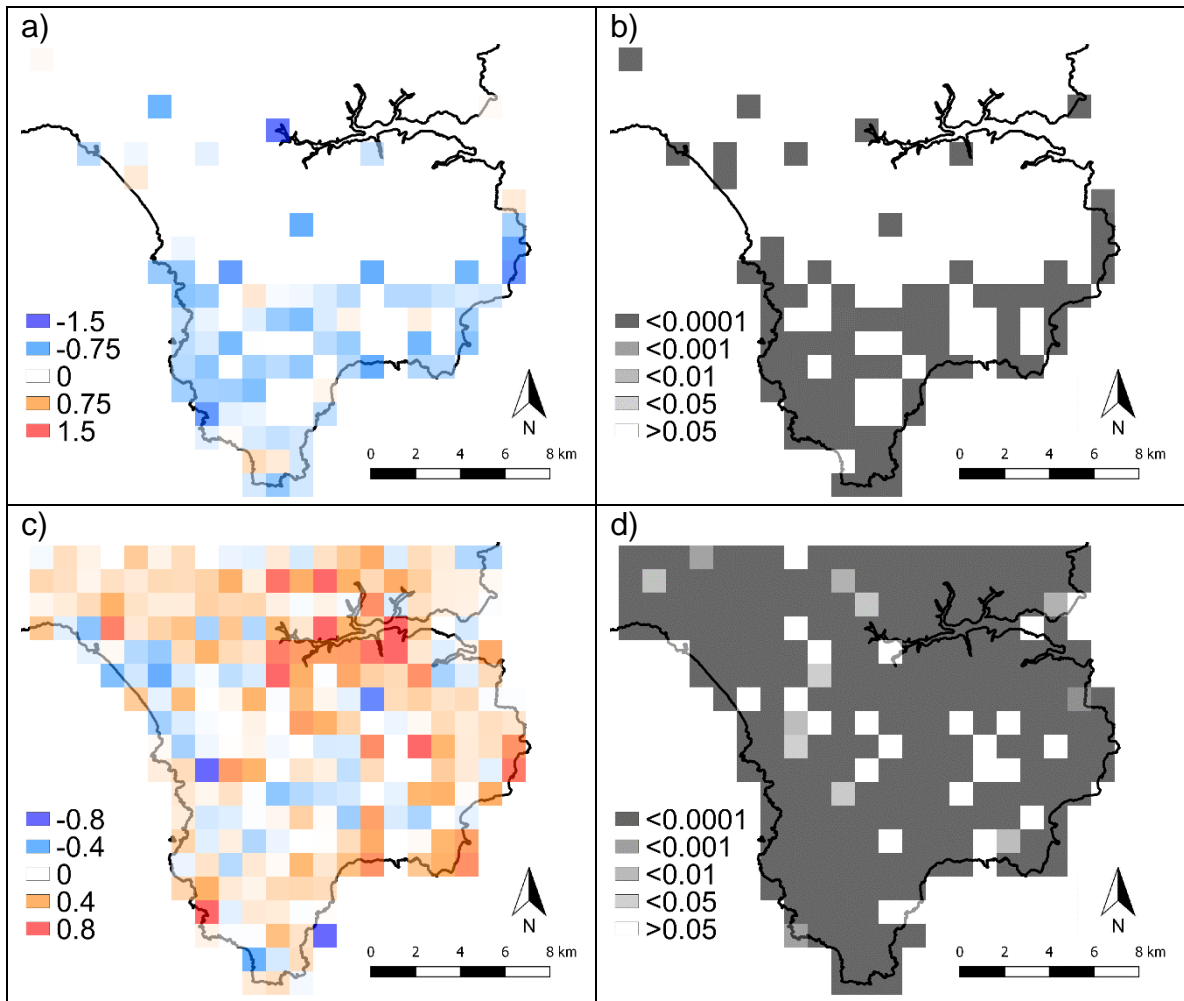


Figure 3. Changes in the moisture index values of each grid cell (a,c), and significance of change (b,d), between successive periods (1900-1985 and 1986-2000) and (1986-2000 and 2000-2013). Frequency histograms of cell changes between periods are provided in Figure S2.2. An increase in moisture index values indicates an increase in plants associated with higher moisture availability in the later period.

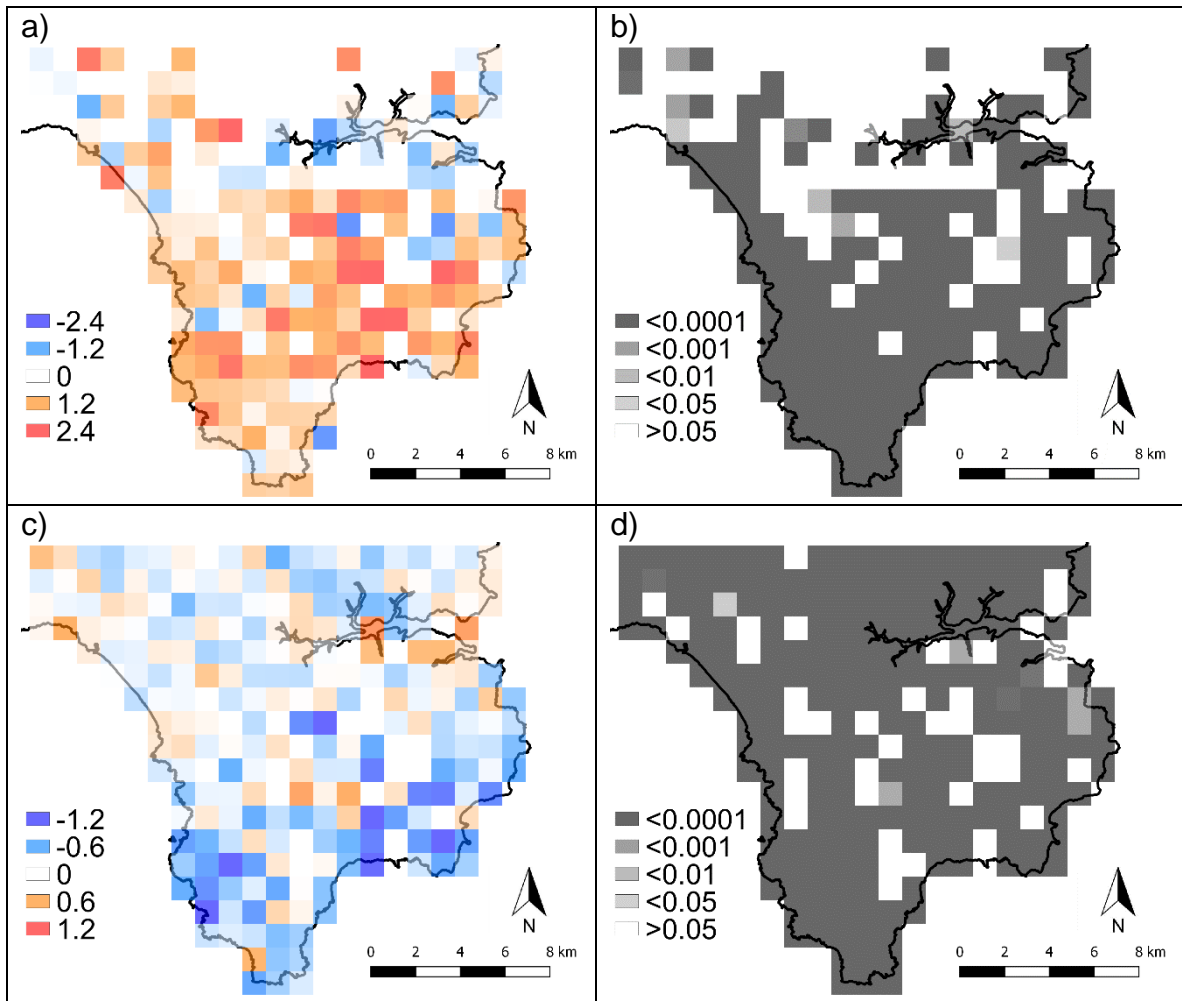


Figure 4. Changes in the nitrogen index values of each grid cell (a,c), and significance of change (b,d), between successive periods (1900-1985 and 1986-2000) and (1986-2000 and 2000-2013). Frequency histograms of cell changes between periods are provided in Figure S2.2. An increase in nitrogen index values indicates an increase in plants associated with higher nitrogen availability in the later period.

Between periods two and three, cell decreases in January and July temperature indices were the result of a sharp decline in the number of records of species with low (but not very low) indicator values (January: Fig. 5b; July: Fig. 6b), whereas cell increases were the result of a balance between both gains and losses (Figs. 5a and 6a). Decreases in cell moisture and nitrogen indices were the result of a balance between both gains and losses, whereas cell increases were primarily the result of gains in species with high indicator values (Fig. 7 and 8).

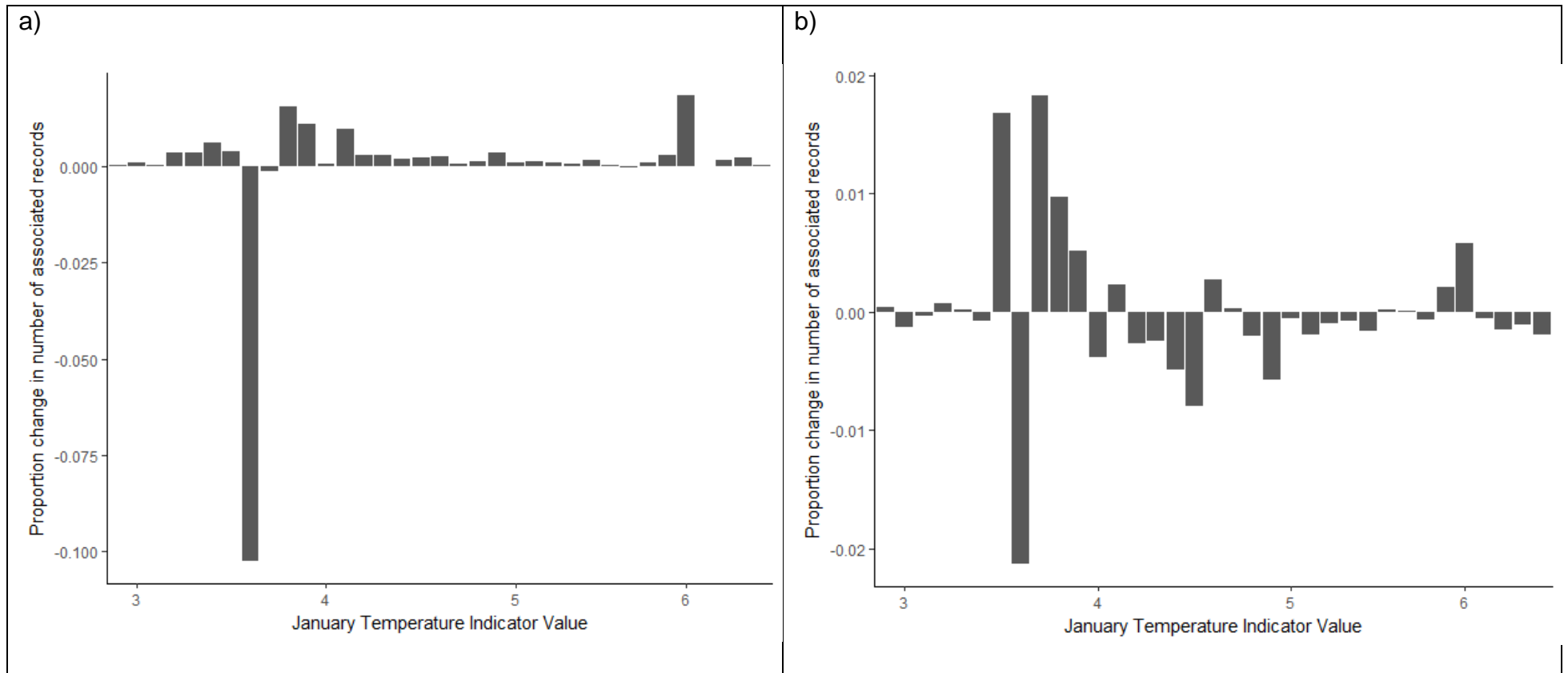


Figure 5. Change in proportion of records associated with a given January temperature indicator value between period two and three in cells which saw an increase in mean January temperature index values (a) and those which saw a decrease (b).

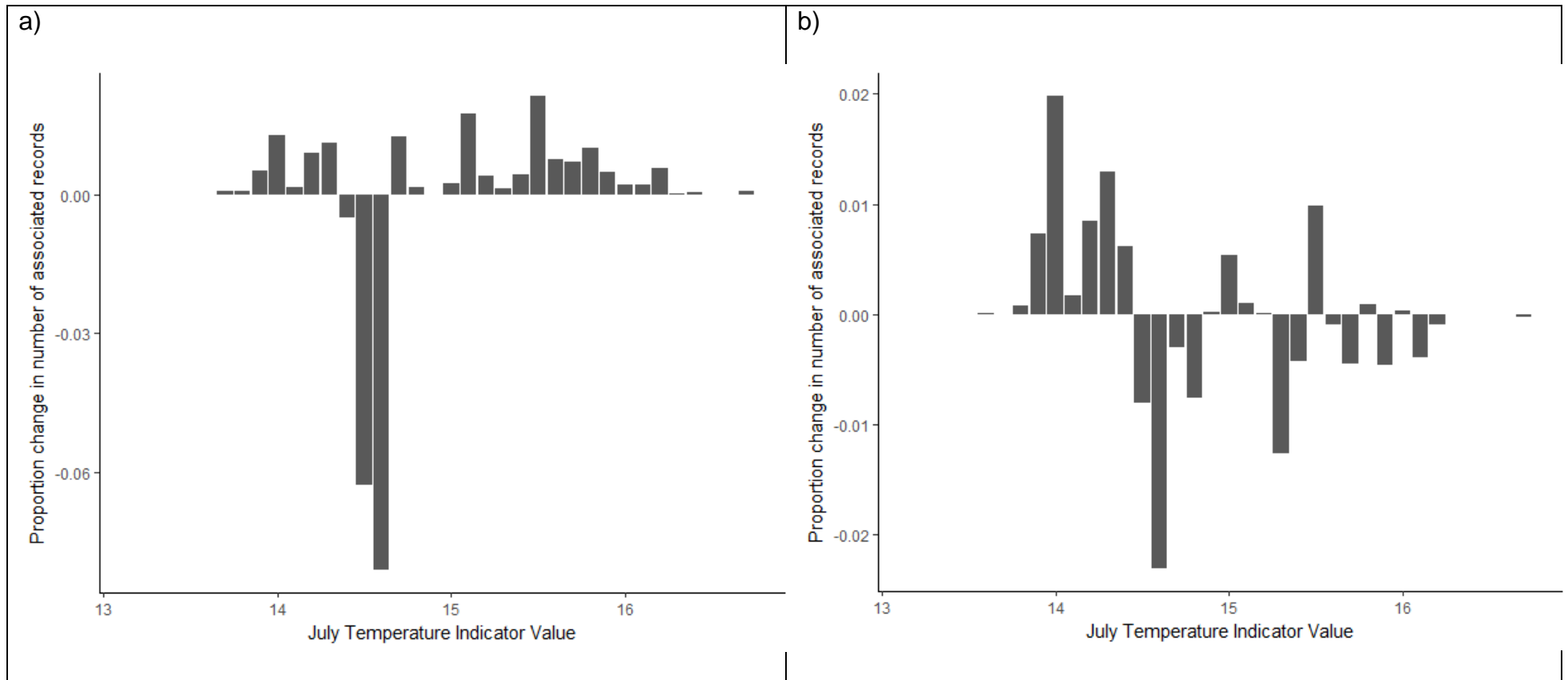


Figure 6. Change in proportion of records associated with a given July temperature indicator value between period two and three in cells which saw an increase in mean July temperature index values (a) and those which saw a decrease (b).

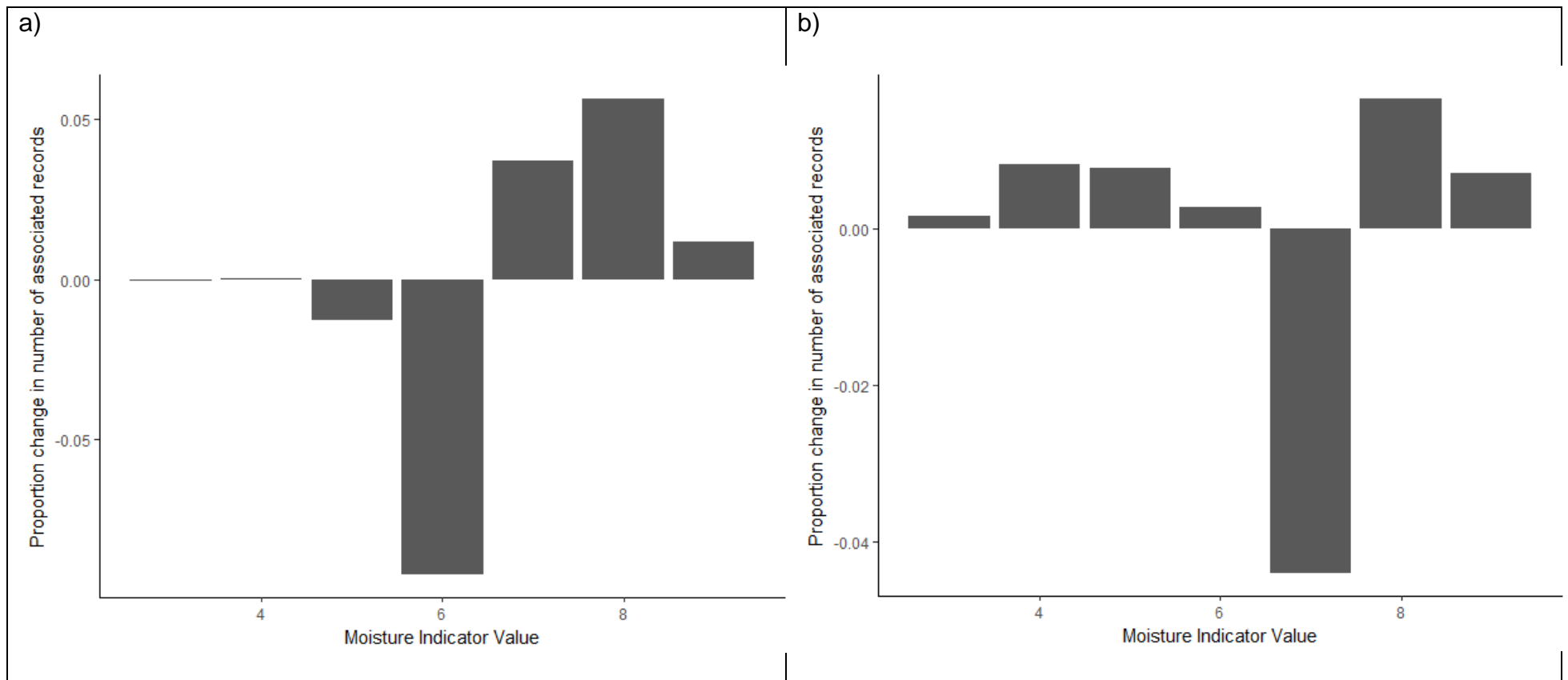


Figure 7. Change in proportion of records associated with a given moisture indicator value between period two and three in cells which saw an increase in mean moisture index values (a) and those which saw a decrease (b).

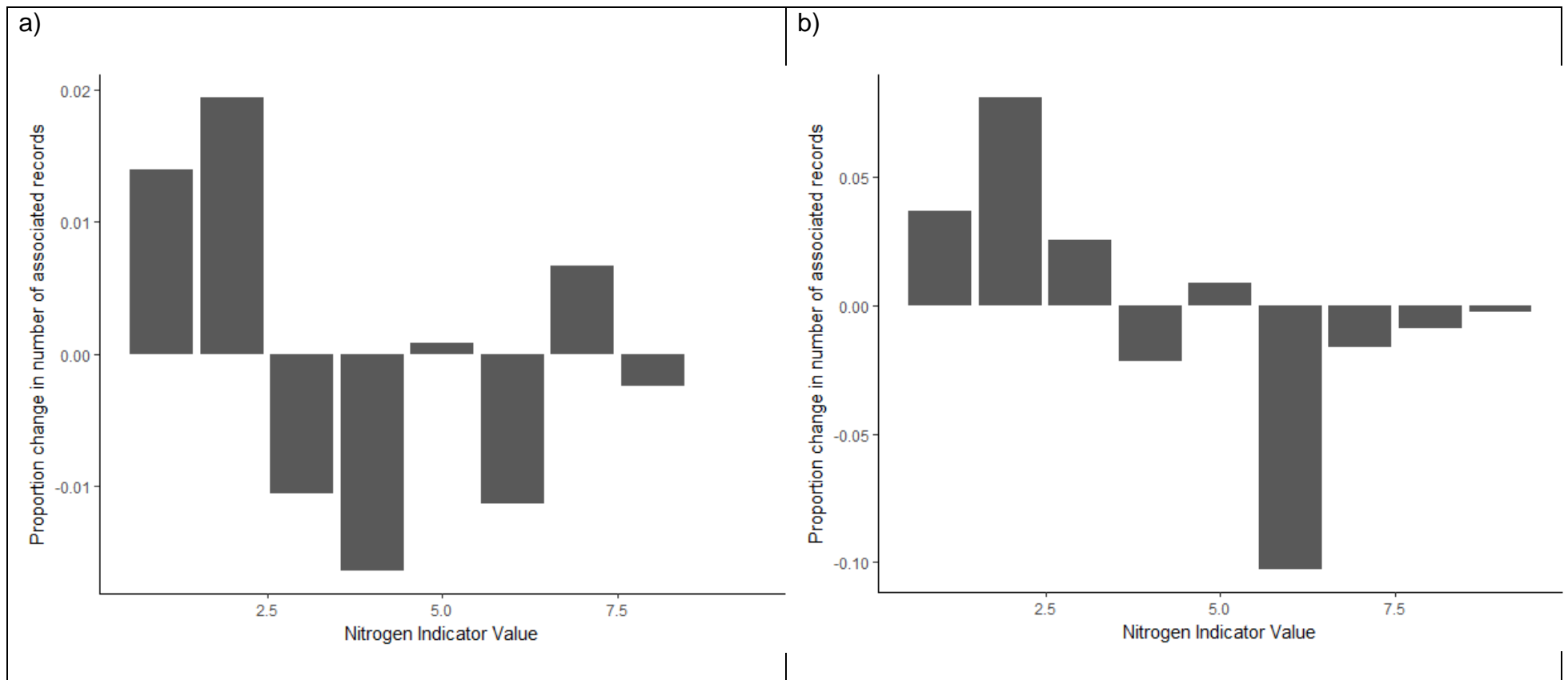


Figure 8. Change in proportion of records associated with a given nitrogen indicator value between period two and three in cells which saw an increase in mean nitrogen index values (a) and those which saw a decrease (b).

Drivers of biodiversity change

Between periods two and three, the model that best explained changes in the January community temperature index (CTI_{jan}) included an interaction between increasing distance from the coast and terrestrial warming, and independent effects of spring solar index, and topographic wetness (Table 1). Changes in the January community temperature index values of grid cells were significantly negatively associated with increasing topographic wetness (Monte Carlo: $p < 0.001$). Increasing distance from the sea resulted in a greater positive effect of terrestrial warming (Monte Carlo: $p < 0.001$).

Between periods two and three, the model that best explained changes in the July community temperature index (CTI_{jul}) included an interaction between increasing distance from the coast and terrestrial warming, and an independent effect of topographic wetness (Table 1). Changes in the July community temperature index values were negatively associated with increasing topographic wetness (Monte Carlo: $p < 0.001$). Increasing distance from the sea resulted in a greater positive effect of terrestrial warming (Monte Carlo: $p = 0.011$).

Between periods two and three, the model that best explained changes in the community moisture index (CFI) included distance from the coast, dominant land cover type, spring solar index, an interaction between terrestrial warming and topographic wetness, an interaction between terrestrial warming and elevation, and an interaction between elevation and topographic wetness (Table 1). Changes in the community moisture index values of grid cells between periods two and three were significantly positively associated with increasing distance from the coast (Monte Carlo: $p = 0.002$), dwarf shrub heath dominant land cover

(Monte Carlo: $p = 0.045$), and inland rock dominant land cover (Monte Carlo: $p < 0.001$). The positive effect of topographic wetness on moisture community index values was lower at higher elevations (Monte Carlo: $p < 0.001$) and greater terrestrial warming (Monte Carlo: $p = 0.038$). The positive effect of terrestrial warming was lower at lower elevations (Monte Carlo: $p = 0.047$). Changes in the community moisture index values of grid a cell between periods two and three were significantly negatively associated with littoral rock dominant land cover (Monte Carlo: $p = 0.005$), freshwater dominant land cover (Monte Carlo: $p < 0.001$), and salt water dominant land cover (Monte Carlo: $p < 0.001$).

Between periods two and three, the model that best explained changes in the community nitrogen index (*CNI*) included distance from the coast, dominant land cover type, spring solar index, and an interaction between elevation and topographic wetness (Table 1). Changes in the community nitrogen index values of grid a cell between periods two and three were significantly positively influenced by salt water dominant land cover (Monte Carlo: $p < 0.001$). Changes in the community nitrogen index values of grid a cell between periods two and three were significantly positively influenced by spring solar index (Monte Carlo: $p = 0.005$), dwarf shrub heath dominant land cover (Monte Carlo: $p < 0.001$), broadleaf woodland dominant land cover (Monte Carlo: $p < 0.001$), and inland rock dominant land cover (Monte Carlo: $p < 0.001$). Increase in elevation significantly increased the negative effect of higher topographic wetness on nitrogen community index values (Monte Carlo: $p = 0.044$).

Table 1. The suite of predictors that best explained changes in community indices between periods two and three, including the intercept and predictors effect on each mean community index value change between periods two and three. Only land uses with significant effects were included. The * indicates significant predictor effects. In land use a is freshwater, b is salt water, c is dwarf shrub heath, d is littoral rock, e is inland rock, and f is broad leaved woodland.

	Intercept	Dist. from sea	Terrestrial warming	Topographic wetness	Dist. from sea x Warming	Spring solar index	Elevation	Land use	Topographic wetness x warming	Elevation x warming	Topographic wetness x elevation
CTI_{jan}	-0.53 ± 0.413	0.118 ± 0.076	0.423 ± 0.371	-0.002 ± 0.007*	-0.114 ± 0.073*	0.673 ± 0.617					
CTI_{jul}	-0.209 ± 0.407	0.114 ± 0.08*	0.287 ± 0.387	-0.007 ± 0.007*	-0.114 ± 0.076*						

<i>CMI</i>	0.165 ± 3.779	0.002 ± 0.007*	0.191 ± 3.651	1.203 ± 1.221*		-4.195 ± 2.533	-0.046 ± 0.042	a: -0.071 ± 0.302* b: -1.065 ± 0.331* c: -0.084 ± 0.087* d: - - 0.477 ± 0.27* e: 0.236 ± 0.31*	-1.046 ± 1.147*	0.059 ± 0.041*	-0.003 ± 0.002*
<i>CNI</i>	0.531 ± 0.8	0.006 ± 0.009		-0.199 ± 0.133*		1.528 ± 3.341*	-0.013 ± 0.007	b: 0.694 ± 0.437* c: 0.207 ± 0.116*			0.003 ± 0.002*

								e: -0.815 ± 0.402* f: -0.052 ± 0.127*			
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Discussion

My findings provide empirical evidence of changes in the floristic communities of the Lizard Peninsula and offer insight into the likely mechanisms driving these changes. Across the period studied, all community index changes varied in response to climate change due to fine-scale spatial and temporal variation in change drivers. The change drivers studied are important aspects of community change globally, suggesting that fine-scale variation is important to consider when predicting community response to climate change.

Patterns of change

Between 1900-1985 and 1986-1999 the community index values associated with warmer summers and winters, and moist conditions decreased, while the community index values associated with nitrogen availability increased. Between 1986-1999 and 2000-2013 the community index values associated with warmer summers and winters, and moist conditions increased, while the community index values associated with nitrogen availability decreased. However, the overall changes between periods two and three were not ubiquitous in the 1 km² cells across the peninsula.

The community changes which resulted in the recorded changes in mean cell community index values were identified. This information helps inform how environmental drivers and other explanatory variables influence variation in community response to a changing climate and changes in land management practices. Analysis indicated that anthropogenic climate change and changes in land use influence changes in the plant community composition. As climate and land use has changed extensively globally over the period investigated, it is likely

that similar environmental changes have occurred more broadly.

Maclea *et al.* (2017), which the terrestrial warming values were derived from, found that warming in winter is greater than in summer on the Lizard peninsula. Additionally, the spatial pattern seen in terrestrial warming on the Lizard was more similar to the pattern seen in the January temperature index value changes than the July temperature index value changes. In areas which experienced the greatest warming, communities had a proportional decrease in records of species associated with low January temperature indicator values. This represents an *in situ*, community level response in species distribution to climate change, and provides evidence that environmental change can be influenced by microclimatic variation.

Despite the recorded decline in water availability from 1979 to 2011 on the Lizard (Maclea *et al.* 2015), there was an increase in moisture index values over the period of study. This doesn't support the prediction that reduced moisture availability will be one of two major drivers of plant species loss by 2080 in Europe (Thuiller *et al.* 2005). Additionally, despite similar findings for other variables, our findings for moisture values contradicts the broader trend across Cornwall found by Kosanic *et al.* (2018). However, there was a trend for moisture index declines in fresh water dominant land cover. The decline in moisture index values in areas dominated by freshwater suggests that moisture availability has declined due to climate change. The observed declines in moisture index values in areas dominated by fresh water were likely the result of a loss of species highly dependent on high water availability. With the decline in water availability since 1979 freshwater sources are likely to have retracted. Thus, species which require

high levels of moisture may have been unable to maintain as a large a population as their limiting resource declined, and so the community response was as expected based on observed ecological change.

In the long term, if water availability continues to decline as predicted, the trend seen in freshwater habitats suggests there will be a decline in species with higher moisture requirements within the community. Additionally, the change maps show the patchy spatial distribution response of moisture index value expected in situations where environmental conditions become drier.

Nitrogen index values tended to decrease over the period of study, suggesting that changes in land use on the Lizard have resulted in reduced nitrogen deposition. However, many coastal cells and areas at lower elevation with high topographic wetness saw an increase in nitrogen index values. The former is likely due to nitrogen run-off from farmland. While agri-environment schemes have promoted reduced nitrogen deposition on the Lizard, it is still used, and run-off is likely carried to coastal regions through rivers (Howarth 2008). When combined with high topographic wetness, the coastal areas with low elevation see even greater increase in nitrogen community index values. This is likely because many species with high nitrogen preferences also prefer high moisture availability (Hill, Preston & Roy 2004), which enables them to dominate the local community when both these resources are abundant. If nutrient enrichment is implemented without control, it leads to a loss of biodiversity (Hejerman *et al.* 2007; Honsová *et al.* 2007). Therefore, looking at nitrogen accretion in coastal areas on the Lizard and further afield may be needed to avoid negative impact

on community resilience and productivity from loss of Biodiversity (Hooper *et al.* 2012).

Change drivers

Climatic changes

To interpret the causes of plant community changes, it is necessary to know the change in climate and land use that happened over a comparable period. This will help identify whether community changes are in direct response to climate driven environmental change, or another driver which might alter climatic influence. Climatic and land use changes are discussed separately to improve readability, with climatic changes being discussed first.

Firstly, January and July temperature index values tended to increase more in cells further from the coast, though the spatial effect of distance from the coast is reduced in cells which experienced greater terrestrial warming. This reinforces previous research, which has found that coastal areas are buffered against the effects of climate change on temperature (Haugen & Brown 1980). Temperature buffering on the coast may allow threatened species with cooler temperature preferences to persist in their current location despite rising temperatures. In consequence, a slower distribution shift away from these areas may be seen in temperature driven changes. However, terrestrial warming's effect on temperature can offset the buffering provided by proximity to the coast. Terrestrial warming varies at the fine-scale in response to solar insolation, supporting the argument that microclimate plays a role in moderating community response to environmental climate change. Overall, this suggests that species distribution shifts in response to temperature increases may not be as rapid as predicted by

coarse-scale models in coastal regions. Species could be occupying microclimatic holdouts, enabling them to persist longer in their current distribution in coastal areas than predicted by coarse-scale. It has been shown that species take advantage of holdouts to persist within areas with unsuitable macroclimatic conditions, for example to live somewhere warmer (Lawson *et al.* 2012), or wetter (Carroll *et al.* 2011). My findings provide another example that supports the idea that predicted species extinction risk may not be as dire as previously reported (Thomas *et al.* 2004). If species are better able to persist in their current distributions despite rising temperatures, it may be that communities are more resilient to change than previously projected.

Secondly, January and July temperature index values tended to increase less in cells with greater topographic wetness. This is likely because areas with higher topographic wetness are more likely to be occupied by species with higher moisture requirements, and these species typically have cooler temperature requirements. This also suggests that in areas with high topographic wetness, species' declines in response to increasing temperatures may be buffered. Species with high moisture requirements would be better able to persist in areas with greater topographic wetness in the face of increasing temperatures. In turn, this would result in greater foliage cover over time, further buffering against temperature changes and moisture loss through greater shading from solar insolation (Morecroft, Taylor & Oliver 1998; Lin 2007). Therefore, as with coastal regions, areas with higher topographic wetness may be predicted to see slower loss of species with cooler temperature preferences. This provides evidence for holdouts in which species cooler temperature preferences could persist in the face of climate change.

There was a decline in records of species with mid-range temperature associations between periods two and three. This decline was likely the result of an inability to tolerate the increasing temperatures and declining moisture availability recorded (Maclean *et al.* 2015). The species with the warmest and coolest temperature preferences on the Lizard are from the Mediterranean and Alpine biomes respectively. Both these biomes are in part defined by low water availability for periods of the year, leading to drought-like conditions. The persistence of species with cooler temperature preferences suggests the ability of Alpine species to tolerate drought-like conditions may be more important than tolerance to rising temperatures. It may be that Alpine species are able to persist in areas with low moisture availability through reduced competition resulting from loss of species less able to tolerate the local conditions.

In terms of cell moisture index values, increases associated with high topographic wetness decreased at higher elevations. These cells also tend to be less nitrogen rich. Areas with higher elevations on the Lizard tend to be further inland and less intensively farmed (Natural England 2017). With less intensive farming there is reduced nitrogen deposition, meaning that species with lower nitrogen requirements are more likely to persist. There are Mediterranean species on the Lizard with lower nitrogen requirements which are often associated with drier habitats. Increased presence of these species due to rising temperatures likely led to the reduced increase in moisture index values observed in areas of high topographic wetness. In addition, temperature increase was less buffered further inland, further increasing the suitability of inland areas for species with preferences for higher temperatures. This information could be used to direct

management practices, as it suggests that topographically heterogeneous areas could be managed to provide suitable habitats for species which require less moisture. Minimising nitrogen deposition in heterogeneous areas could benefit less competitive species with lower moisture preferences. This is particularly beneficial for species with extreme temperature preferences due to the more extreme average temperatures in topographically heterogeneous areas. Areas with many north-facing slopes provide cooler mean and maximum temperatures and can be manipulated to have reduced moisture availability. This would create areas for species with cooler temperature preferences and low moisture requirements to persist in the face of climate change.

Moisture index values were also found to increase less in areas which have high topographic wetness and terrestrial warming. This might be explained by the increase in evapotranspiration seen in warmer areas, though this is an area of contention (Barnett, Adam & Lettenmaier 2005). The loss of moisture through increased evapotranspiration will result in local decrease in moisture availability, leading to habitat becoming unsuitable for species with high moisture requirements. This suggests that as temperature continues to rise because of climate change, prevalence of species associated with high moisture levels will continue to decline. On the other hand, mean moisture community index values tended to increase in cells further from the coast. This was likely due to the greater abundance of sheltered locations further from the coast resulting from less focused vegetation management of these areas. With more shelter there is reduced solar insolation due to shading, which reduces evapotranspiration (Moeslund *et al.* 2013). Consequently, there is more available moisture, enabling species with high moisture associations to persist. It may be that by increasing

the number of sheltered locations it would be possible to buffer the loss of species with high moisture requirements from areas with greater terrestrial warming.

Nitrogen index values tended to increase at lower elevations with greater topographic wetness. When released from moisture and nitrogen constraints at lower elevations, species with higher nitrogen tolerances are better able to compete for resources than species adapted to nitrogen poor conditions (Stevens *et al.* 2004). This would result in the observed increase in nitrogen index values. Additionally, an increase in plants that have higher nitrogen preferences is also likely to increase sward height due to the promotion of growth resulting from high nitrogen availability (Lawlor, Lemaire & Gastal 2001). As a result, the mean microclimatic temperature of these areas will increase less due to greater canopy shading (Morecroft, Taylor & Oliver 1998; Lin 2007). This may explain the increased prevalence of species with low temperature associations in areas with greater nitrogen availability. While communities in such areas may be buffered from temperature increases, previous studies looking at the active use of nitrogen enrichment found a negative impact on biodiversity as a result of a decline in species richness (Foster & Gross 1998; Hejman *et al.* 2007; Honsová *et al.* 2007). As such, while shading appears to offset macroclimatic temperature increases, care needs to be taken when considering it for *in situ* management (Greenwood *et al.* 2016).

While it is possible to explain observed environmental changes due to climate change, it's often hard to distinguish climate change effects from successional change in plant communities. Vegetation changes may be indicative of successional change, rather than climate change in fragmented, semi-natural

grassland (Bennie *et al.* 2006). My results support their findings that topographic heterogeneity has a marked effect on microclimate in grasslands, and consequently the resistance of vegetation to change. In areas with lower topographic heterogeneity, microclimate varies less. Consequently stress-tolerant species (i.e. colonist species) may decline in occupancy as more competitive species succeed them. On the other hand, areas with greater topographic heterogeneity will have more varied microclimates, and so habitats with suitable microclimates for stress-tolerant species are more likely, resulting in their extended persistence. Thus, it may be that variation in the community changes observed are the result of differences in rates of successional change rather than climate change, though microclimate still plays an important role.

Land use changes

The temperature change maps between periods two and three suggest that in agriculturally unimproved, urbanised, and exposed areas the expected influence of increasing temperatures resulting from climate change is greater. This was determined by overlaying them on to Natural England's MAGIC maps (2017) land use layer. The map of land use shows what different areas of the Lizard are used for, and which schemes they are managed under. In exposed areas we see greater increases in temperature index values on average, suggesting they provide suitable habitats for species with higher temperature preferences as temperatures continue to increase. This suggests that if sheltering exposed habitats was encouraged, species with cooler temperature preferences would be more likely to be able to persist. On the broader scale, these findings have important implications for the environmental responses to climate change. If we know that more exposed areas experience greater temperature increases, they

could be utilised as stepping stones for species distribution shift. Stepping stones would enable isolated species to shift their distribution, and so keep pace with temperature increases resulting from climate change. Alternatively, if the plant community in an area is likely to be heavily negatively impacted by increasing temperatures, steps could be taken to reduce the number of exposed areas to maximise habitat availability.

Moisture community index values tended to decrease in cells dominated by littoral rock or salt water (i.e. coastal cells) and dwarf shrub heath. This was likely due to the limited moisture availability in such areas being exacerbated by the decline in water availability on the Lizard between 1979-2011 (Maclean *et al.* 2015). This would lead to the loss of mid-range moisture dependant species recorded (Fig. 7). Interestingly, moisture community index values have also tended to decrease in cells dominated by fresh water. This might be because the sources of fresh water have receded over the period observed, due to reduced rainfall, resulting in less available moisture for plants. It may also be due to reduced dry-season water availability (Barnett, Adam & Lettenmaier 2005). If a species' growth period is during the dry season, then the increasing decline of available water during this period may narrow its' window of opportunity for growth and propagation. This may have prevented species with mid-range moisture requirements from having a long enough growth period to reproduce effectively and so persist in the community. Moisture community index values tended to increase in cells dominated by inland rock. This might be because access to these areas is difficult. As a result, management to remove dense foliage for the benefit of less competitive, rarer species on the Lizard has not been applied. This would result in reduced removal of plants with high moisture requirements, leading to the

observed increase in moisture index values in areas dominated by inland rock. As previously mentioned, dense foliage provides shading, reducing solar insolation. With lower solar insolation there is reduced evapotranspiration (Bois *et al.* 2008), and so species with high moisture requirements could persist.

Nitrogen index values tended to increase in coastal cells and decrease when cells were dominated by dwarf shrub heath, broadleaf woodland or inland rock land cover. The increase in cells by the coast was likely the result of nitrogen runoff from nearby intensively farmed land, as explained previously, increasing nitrogen availability in coastal grassland and heath at lower elevations (Howarth 2008). Due to this nitrogen run-off, species which rely on high nutrient availability can occupy habitats that would otherwise be unsuitable. The introduction of the Countryside Stewardship Scheme in 1991, now the Environmental stewardship scheme was an attempt to mitigate nitrogen runoff and appears to have been effective outside of cells along the coast. The agri-environment schemes were strongly promoted on the Lizard and now cover more than half of the peninsula (Natural England 2017). The agri-environment schemes encourage more sustainable use of the land, including (i) conserving biodiversity; (ii) improving water management and quality; and (iii) improving soil management. In practice on the Lizard this resulted in a combination of managed grazing and scrub clearing, particularly in biodiversity rich areas (Pearman 2017), as well as reduced fertiliser deposition on farmland. The combination of reduced artificial fertilisation deposition with active land management aims to promote floral diversity, as in other areas of the UK (Young *et al.* 2005). Reduced nitrogen deposition also likely led to the overall observed increase in nitrogen intolerant species and decrease in nitrogen tolerant species on the Lizard. Plant growth is

also reduced with reduced nitrogen deposition (Ingestad 1977), thus providing provide less vegetation cover. Areas with little vegetation cover typically experience higher mean soil temperatures (Morecroft, Taylor & Oliver 1998), and greater fluctuations in air temperature (Lin, 2007). This is likely why areas with more exposed habitats and reduced nutrient enrichment were found to have a greater abundance of species with higher temperature associations. The majority of species with warmer temperature associations on the Lizard are associated with the Mediterranean biome, which has greater species richness than most temperate regions (Cowling *et al.* 1996). These findings suggest that agri-environmental schemes can be used to manipulate microclimatic conditions to promote biodiversity through canopy cover manipulation and nutrient availability. Through managed grazing and scrub clearing, areas can be cleared to allow less competitive species to occupy them. By limiting nitrogen deposition species which can take advantage of nutrient availability to grow faster are less likely to dominate an area, thus avoiding a monoculture and loss of biodiversity.

There were also cells in which the mean community index values for both temperature and nitrogen associations have declined. These cells, though few, are typically located in areas with greater topographic heterogeneity. These areas are largely rocky outcrops, heath and unimproved grassland. The reason for the difference in prevalence of species with cooler temperature associations is likely due to land use. Topographically diverse areas cannot be farmed as easily, due to lack of accessibility and difficulty in application of farming tools. Additionally, topographically diverse areas on the Lizard are often particularly botanically interesting (Pearman 2017), and so will have been subject to greater conservation management. Both land management situations would result in

reduced nitrogen deposition. There are alpine species on the Lizard which have lower temperature preferences and are also better suited to lower nutrient availability, and so benefit from the reduced nitrogen availability. That temperature index values also decreased in topographically diverse areas suggests there is a high availability of north facing slopes. North facing slopes experience cooler average temperatures and so provide suitable microclimates for species with cooler temperature associations (Weiss, Murphy & White 1988). This explains the observed temperature index value decline in these areas despite the decline in nitrogen index values. These findings suggest that if nitrogen deposition can be limited in topographically diverse areas, they may provide microclimatic holdouts for species with lower temperature preferences and nitrogen dependence.

Conclusion

In conclusion, the change maps provide important insights in to the processes which drive the ecological responses to climate change. The community changed in response to temperature, as well as moisture and nitrogen availability. None of the community responses were ubiquitous across the Lizard peninsula but showed patchy spatial distribution due to variation in topographic wetness, terrestrial warming, coastal proximity and land use over the past 113 years. The varied community response to climate change across the Lizard highlights the complexity of climate change and land uses' influence on environmental change, and thus biodiversity. Consequently, this suggests that the predicted loss of species through climate change is not as clear cut as originally thought and is likely influenced by microclimatic variation. As such, understanding responses to climate change at very fine spatial scales (10 metres) could help to identify and model climatic effects at the scale organisms typically experience them (Potter,

Woods & Pincebourde 2013). This study helps to identify the environmental drivers of the observed changes, as well as identify that environmental changes at the scale of 1 km differ from changes across the wider area that encompasses those localities (e.g. 10 km). If fine-scale changes do differ from coarse-scale ones, then there is support for the idea of microclimatic refuges. If there are areas that maintain a suitable microclimate despite climate change, then habitat may remain in which species can persist. Examples of such areas in the study region include coastal regions, and those with heterogeneous topography. If microclimate plays a role in determining species distributions, then coarse-scale models may be unsuitable to predict changes in species distribution due to climate change. Particularly in heterogeneous environments, coarse-scale distribution models would not account for the fine-scale environmental variation leading to microclimatic diversity. Thus, the types of patchy community response described by this study would not be accounted for, and so predictions of species distribution changes would be inaccurate. This would lead to inaccurate predictions of biodiversity loss due to climate change, as well as potentially misleading efforts to conserve biodiversity through management.

Chapter 3: The influence of microclimate of species distribution

Summary

1. Assessing the determinants of species geographic distributions, and their likely response to climate change, is fundamental to many aspects of ecology, biogeography, and conservation biology. Though it is well known that climate affects species distributions at coarse spatial resolution, it is still widely perceived that patterns of distribution at a fine-resolution are determined by factors other than climate, such as habitat availability and biotic interactions. However, surprisingly few studies have tested this perception. Here I examine whether climate at fine spatial resolution (5m), or microclimate, is important in determining the distributions of species with a broad range of biogeographic associations on the Lizard Peninsula, United Kingdom.

2. I examine the factors affecting the 5m distributions of 20 plant species. I assess the relative importance of microclimatic conditions in shaping the distributions of plants at the colder limits of their geographic range relative to those at the warmer limits. Microclimate was determined by solar coefficient, calculated using slope and aspect of each 5m site, and sward height.

3. Despite a weak positive association between the macroclimatic associations and microclimatic requirements of species, species at both the cold and warm limits of their range occurred in the warmest microclimates available. Rarer UK species occupied microsites with significantly lower surrounding sward height.

4. *Synthesis and applications.* Local climatic conditions affect local patterns of plant distribution. Both continental species at the cooler extremes of their

geographic range and boreal species at the warmer extremities of their range preferred warm microclimates, suggesting that coarse-scale species distribution modelling may give a misleading picture of species responses to climate change.

Key-words: coastal grassland, flora, global warming, insolation, microclimate, topoclimate

Introduction

Understanding the determinants of species geographic distributions, particularly climate, is a key goal of ecology, and crucial for predicting ecological responses to climate change. To date most estimates of the threat of climate change to biodiversity have relied on species distribution models (SDMs) that have calculated spatial associations between species distributions and climate variables at coarse spatial scale, i.e. tens to hundreds of kilometres. Results from these models suggest catastrophic consequences for life on earth as a result of anthropogenic climate change, predicting for example, that by 2050 between 15 and 37% of species will be committed to extinction (Thomas *et al.* 2004). Thus far, however, climate change has been implicated as a major cause of the loss of just nine species (IUCN 2017). This discrepancy may be because the conditions many organisms experience are over scales from millimetres to tens of metres (Potter, Woods & Pincebourde 2013), which are not captured in coarse-scale SDMs. Particularly in temperate regions, there is considerable fine-resolution spatial variation in climate caused by differences in topography and vegetation cover. Empirical studies show that these fine-resolution spatial differences in temperature can be as large as inter-continental differences that are measured at coarser resolutions. For example, on south-facing slopes surface temperatures

can be as much as 20°C warmer than nearby air temperatures (Bennie *et al.* 2008). Even over short distances of a few metres, conditions can vary from permanently wet to permanently dry (Maclean *et al.* 2012). Vegetation cover and canopy shading also cause substantial variations in temperature, with recorded differences among habitats of more than 5°C in monthly temperature maxima and minima, and of 10°C in thermal range (Suggitt *et al.* 2011).

The mismatch between the spatial scale at which an organism experiences climate and the resolution at which the relationship is typically modelled, has important implications for the accuracy of SDM predictions. For example, if microclimate (e.g. five-meter resolution) influences distribution analogously to macroclimate (e.g. greater than one-kilometre resolution) we would expect species at the cold limits of their range to occupy warm microclimates and vice-versa. If this expectation is correct, then an area that a coarse-scale SDM predicts to be too cold for a species could in fact be occupied if within that area there were localities that have the species' preferred microclimate. These areas would therefore be more likely to retain or be colonised by species in a changing climate. As a result, coarse-resolution SDMs would provide inaccurate predictions in the face of climate change; fine-scale climatic variability could allow species to persist in their current range under a changing climate. Moreover, microclimatic conditions do not necessarily conform to the simple latitudinal or altitudinal gradients that macroclimate typically does. For example, regions with a cool macroclimate could still contain a substantial number of areas with warmer microclimates. Consequently, species may simply shift the distribution around a hillside, rather than be completely lost from an area as predicted by coarse-resolution models. This suggests that conservation measures such as the

redesign of protected area networks (Araújo *et al.* 2011) or species translocations (Thomas 2011) may be less urgent than is commonly perceived. Indeed, current protected areas have been shown to be valuable at trailing-edge warm range margins (Gillingham *et al.* 2015). Thomas & Gillingham (2015) argue that management within pre-existing protected areas may slow climate-related declines. Given that range expansions have been documented far more frequently than range contractions (Sunday, Bates & Dulvy 2012), it may be that microclimate plays a vital role in enabling species to persist in a warming climate at the trailing edge of their range.

While findings suggest that microclimate affects species distribution, there is much disagreement with regards to how it does this. Some argue that, to a certain extent, the mismatch between the resolution at which a species experiences its environment and the spatial resolution of distribution models is bridged implicitly in most SDMs. This is achieved with a 'mean field approximation', by assuming that grid-cell average climatic variables reflect the aggregate effects of local-scale temperature on fitness, population dynamics and hence on species distributions (Bennie *et al.* 2014). Others argue that, at fine-resolution, microclimate is relatively unimportant in determining species distributions, in comparison to other factors such as biotic interactions (e.g. Pearson and Dawson 2003). Where the effects of resolution have explicitly been tested, some authors have shown that fine-scale models predict greater species persistence in comparison to coarse-scale models (Randin *et al.* 2009), whereas others show entirely the reverse pattern (Trivedi *et al.* 2008). Gillingham *et al.* (2012) show that spatial resolution is also important at lower elevations, and while fine-resolution models provide more accurate estimates of expected patterns of

change, it is not a straightforward topic. A further complexity is that climatic and non-climatic factors can act together and be hard to distinguish. For example, in Arctic-alpine plants, those which would be expected to retract their range under climate change are often adapted to the harsh conditions associated with open habitats. This prevents Arctic-alpine species from occupying other habitat types through competition with larger plants (Choler, Michalet & Callaway 2001; Liancourt, Callaway & Michalet 2005; Birks 2008; Kudo *et al.* 2017). In the open habitats Arctic-alpine plants occupy, the temperatures are on average warmer than those where direct solar radiation is blocked by canopy shading (Suggitt *et al.* 2011). This is counter to Arctic-alpine species' macroclimatic associations. Such locations are also defined by rapidly fluctuating moisture availability (Penna *et al.* 2009). This variation in temperature and water availability, rather than higher mean temperatures, may be responsible for excluding potential competitors from these locations (Billings & Mooney 1968). Consequently, microclimatic variation as seen in the above examples may influence species distributions at a scale which cannot be measured by mean-field approximation in coarse-scale SDMs. This will result in inaccurate predictions for changes in species distribution, particularly in heterogeneous habitats.

I set out to establish the extent to which microclimate influences the distribution of a range of plant species associated with the coastal grassland and heathland of the Lizard Peninsula, UK. Chosen species ranged widely in their temperature and moisture associations. Species with differing associations were used to identify the most important aspects of microclimate across a broad macroclimatic range. Specifically, I focus on the influence of fine-scale site structure as defined by (i) slope and aspect, which influence local temperature and soil moisture - and

(ii) sward height, which influences local surface temperatures through canopy shading and buffering wind speed. In temperate regions these are the main influences on local temperatures and soil moisture (Bennie *et al.* 2008; Suggitt *et al.* 2011). I further aim to test the relationship between species' macroclimate associations and the microclimatic conditions they occupy: are species with the warmest macroclimatic temperature associations (Mediterranean species) confined to steep, south-facing slopes with short sward height and hence particularly warm microclimates? Conversely, are species with the coolest macroclimatic temperature associations (Arctic-alpine species) confined to the shallow slopes with high swards and hence cool microclimates? In so doing, I aim to determine the importance of microclimate in shaping species distributions. I also aim to shed light on the extent to which fine-resolution climate data are likely to be needed for accurate forecasts of species distribution shifts under climate change.

Methods

Study System

The study was conducted on the coastal grasslands of the Lizard Peninsula in Cornwall, United Kingdom (UK; 50.143°N, 5.124°W). Relative to elsewhere in the UK, the climate in this area is characterised by mild winters and dry summers. The grasslands cover a variety of different bedrock types, including serpentine, hornblende and mica schists, and in a few places, felsic rock and sandstone (Fig. 1).

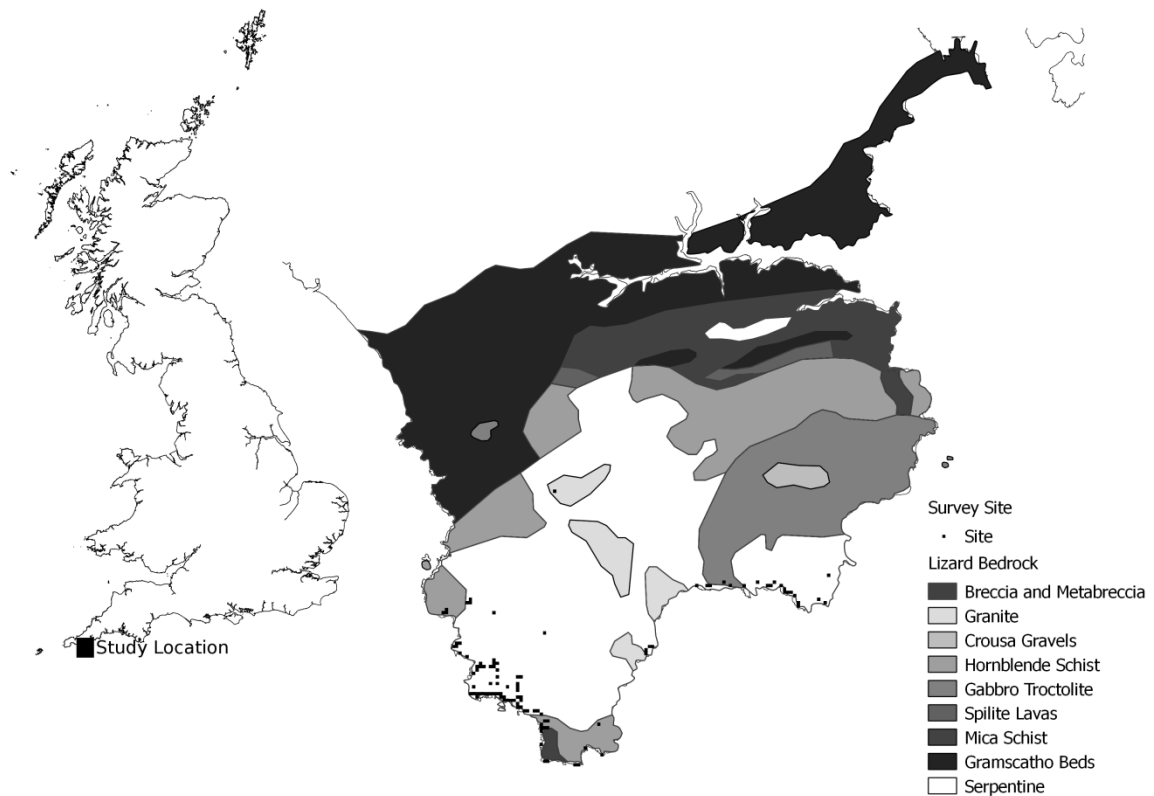


Figure 1. Location of the Lizard Peninsula (left) and a map of the geological bedrock of the Lizard Peninsula with survey site locations (right), based on the British Geological Survey bedrock map. Contains OS data © Crown copyright and database right (2016).

Twenty species were selected for survey with the aim of including much of the specialist flora of the Lizard Peninsula. Species selection also ensured that the species included encompassed a broad spectrum of temperature associations. Selected species are found in a variety of major biomes in Europe (Hill *et al.* 2004; Table 1). Selection was done in this way to determine the difference in microclimate preferences across macroclimatic associations.

Initial narrowing of focal species was done by flowering period, ensuring they flowered within the May to September survey period. *Allium schoenoprasum* was

selected as the representative species for the Boreo-arctic Montane biome as it was one of only two choices and the other, *Leymus arenarius*, had only four records on the Lizard. Similarly, *Minuartia verna* was selected to represent the Boreal-montane biome as it was one of only 5 species, and the others all had fewer than 20 records on the Lizard. *Campanula rotundifolia* and *Sanguisorba officinalis* were selected to represent the Boreo-temperate biome as the Lizard is a hotspot for both species within Cornwall. The Lizard is also a hotspot in UK for the species selected to represent the Temperate, Southern-temperate and Mediterranean biomes, with the exception of *Trifolium striatum* and *Trifolium subterraneum*. These last two species were chosen due to their relative rarity on the Lizard in comparison with their overall distribution, suggesting a potentially interesting localised climatic limitation in their distribution.

Table 1. The coastal grassland species surveyed on the Lizard Peninsula, with their macroclimatic temperature associations (January and July temperature indicator values) and major biome (Hill, Preston & Roy 2004; Fig. 2), and the number of individuals surveyed for each species.

Species (abrv.)	January temp (Tjan)	July temp (Tjul)	Major biome (E1)	Number of individuals
<i>Allium schoenoprasum</i> (A.s)	4°C	14.9°C	Boreo-arctic Montane	205
<i>Asparagus officinalis</i> <i>subsp. prostratus</i> (A.p)	5.9°C	15.9°C	Temperate	140
<i>Campanula rotundifolia</i> (C.p)	3.2°C	14.4 °C	Boreo-temperate	146
<i>Cytisus scoparius</i> (C.s)	3.4 °C	14.6 °C	Temperate	82
<i>Erica vagans</i> (E.v)	6 °C	15.5 °C	Southern- temperate	202
<i>Filipendula vulgaris</i> (F.v)	3.6 °C	15.8 °C	Temperate	213
<i>Genista pilosa</i> (G.p)	5 °C	15.6 °C	Temperate	165
<i>Herniaria ciliolata</i> (H.c)	6.5 °C	16.2 °C	Southern- temperate	196
<i>Hypochaeris maculata</i> (H.m)	3.9 °C	16.1 °C	Temperate	89
<i>Juncus capitatus</i> (J.c)	6.3 °C	16.1 °C	Southern- temperate	27

<i>Minuartia verna</i> (M.v)	2.7 °C	13.9 °C	Boreal-montane	225
<i>Orobanche alba</i> (O.a)	4 °C	13.7 °C	Temperate	202
<i>Sanguisorba officianalis</i> (S.o)	3.2 °C	15.1 °C	Boreo-temperate	205
<i>Scilla autumnalis</i> (S.a)	5.9 °C	16.2 °C	Mediterranean	200
<i>Trifolium bocconeii</i> (T.b)	6.5 °C	16.2 °C	Mediterranean	70
<i>Trifolium incarnatum</i> <i>subsp.molinerii</i> (T.m)	6.4 °C	16.4 °C	Mediterranean	241
<i>Trifolium occidentale</i> (T.o)	6.3 °C	15.9 °C	Temperate	265
<i>Trifolium striatum</i> (T.s)	4 °C	15.7 °C	Southern- temperate	208
<i>Trifolium strictum</i> (T.stc)	5.8 °C	15.9 °C	Mediterranean	84
<i>Trifolium subterraneum</i> (T.su)	4.5 °C	16.2 °C	Mediterranean	95

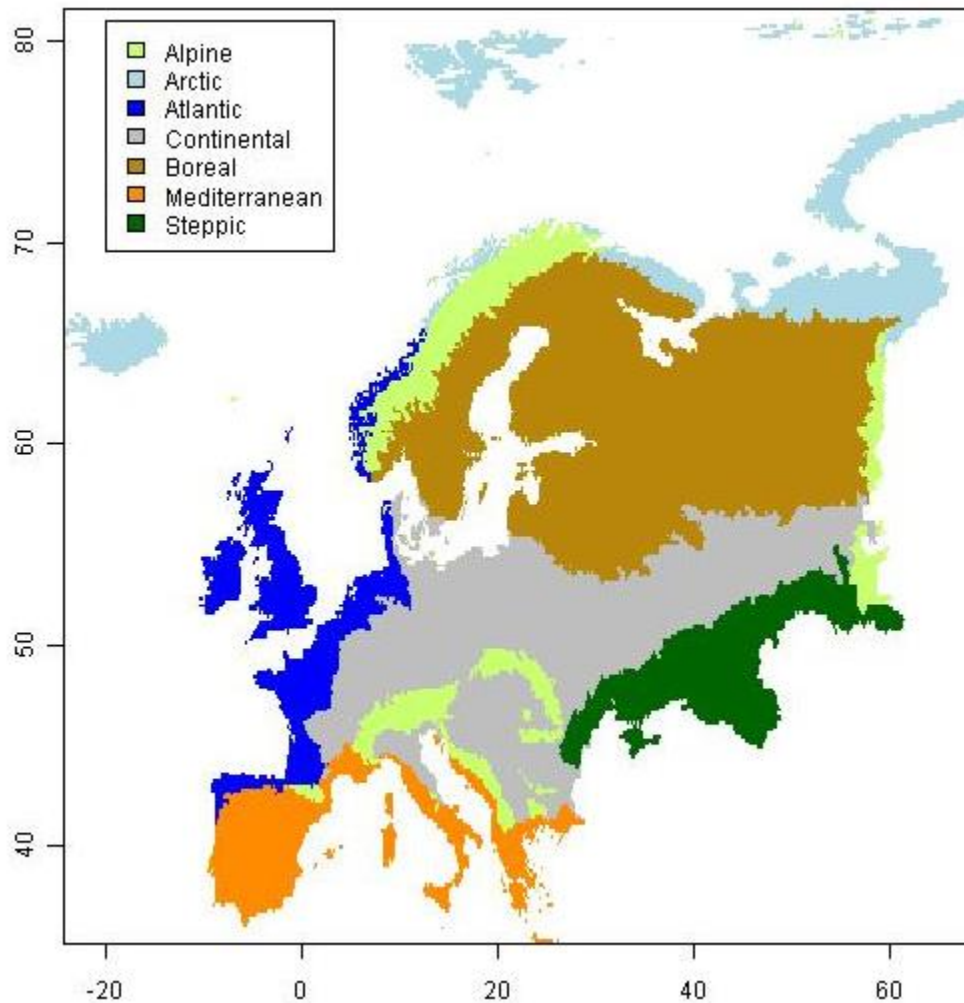


Figure 2. Map of species' major biomes, based on biogeographical regions (Early & Sax 2014). Copyright © 2017 John Wiley and Sons (reproduced with permission - see appendix).

Survey Methods

Surveys were carried out between May and September 2013. Sites at which target species were historically present were determined using records from the ERICA database (French 2010), which manages natural history records in Cornwall. Historically occupied sites were chosen to maximise the number of species occurrences we could document during the field season. However, species distributions may have changed since the historical sites were identified.

Therefore, to study presence and absence outside the historical sites, random encounter surveys were carried out. Random encounter surveys consisted of walking coastal paths at an even pace until a target species was sighted and the individuals' environmental details recorded.

When a target species was found, the location of the species was recorded using a GPS to 5m accuracy, and a 5m² quadrat was centred on the originally identified specimen. In each quadrat the following measurements were taken: (i) the slope and aspect of the steepest gradient was recorded using a digital inclinometer and compass, (ii) soil depth up to 25cm measured in the immediate vicinity of the specimen, (iii) vegetation cover based on the percentage of bare ground observed, (iv) sward height estimated from the mean of four ruler measurements at random locations within the quadrat. Once an initial target species specimen had been located, any additional specimens of target species were searched for within the 5m² quadrat. A 0.5m² quadrat, sub-divided by a 10cm² grid, was centred on each focal specimen and the same field measurements taken for slope, aspect, soil depth, and vegetation cover and height within this smaller quadrat. Each specimen within a 5m² quadrat was used as a separate data point for analysis. Up to 20 individuals per species were used to record environmental variables per 5m² quadrat. It was felt that adequate habitat variation in a 5m² quadrat could be accounted for by measuring environmental variables around 20 individuals per species. This allowed for more species sites to be studied in the narrow presence window for many species across a broader range of habitats. In turn, this enabled observation of the greatest number of different locations each species occupied while getting enough measurements of individuals.

To provide a proxy of microclimate in each quadrat, the proportion of potential direct irradiance intercepted by the surface for a given solar zenith and azimuth (hereafter referred to as insolation) was calculated as follows:

$$Ri = \cos S \cos Z + \sin \beta \sin Z \cos(\Omega_s - \Omega)$$

where Ri is the proportion of potential direct irradiance intercepted by the slope, S is the angle of the slope, Z is the solar zenith, Ω_s is the solar azimuth and Ω is the slope aspect. The solar zenith and azimuth are functions of latitude Julian day and were derived using methods detailed in Hofierka (2002) and Bennie *et al.* (2008). The mean value for every hourly period between 1st of April and 1st of August was used, as this period corresponds to the growing season of targeted species. Solar insolation was used as a proxy of air temperature as the two correlate very strongly, particularly in the summer (Maclean *et al.* 2017). The solar insolation coefficient of an area provides an effective proxy for microclimate, as solar insolation influences near-surface temperatures, evaporative demand, and soil moisture (Bennie *et al.* 2008).

For each species, specific January and July temperature associations, the major biome with which they are associated, and UK abundance were obtained from the PlantAtt database (Hill *et al.*, 2004). January and July temperature associations are based on the average January and July temperatures of all 10km squares in which the plants are present across Britain, Ireland and the Channel Islands. The major biomes are based on European geographical distribution and floristic elements (Preston & Hill 1997) and range from Boreo-Arctic Montane, hereafter Arctic-alpine, to Mediterranean (Table 1). UK

prevalence is based on the number of occupied 10km cells by each species across the British Isles and the Channel Islands (Hill, Preston & Roy 2004).

Data Analyses

To test the relationship between the solar insolation coefficient of areas occupied and species' macroclimatic temperature associations a linear mixed effects model was used. The interactive effect of temperature associations, soil depth, and sward height on the solar insolation of an area species occupied was modelled for both January and July temperature associations in separate models. Sample quadrat was used as a random intercept to account for data non-independence in both models. This relationship would be coded in R as Solar insolation coefficient ~ Temperature association * Soil depth * Sward height + (1 | Quadrat).

To test the relationship between the solar insolation of areas a species occupied and a species' major biome a linear mixed effects model was used. Sample quadrat and species were used as random intercepts to account for data non-independence. This relationship would be coded in R as Solar insolation coefficient ~ Major biome + (1 | Quadrat) + (1|Species).

Solar insolation coefficients were subject to BoxCox transformation to achieve normality of residual distribution for these models. The MuMIn package for R (Barton 2016; R Core Team 2016b) was used to perform a model dredge to identify the suite of predictors that best explained the observed solar insolation coefficients of the different species.

To test the relationship between the number of 10km cells species occupy across the British Isles and the Channel Islands and the interactive effects of sward height of areas a species occupied and species' January and July temperature associations as separate interactions a linear mixed effects model was used. Sample quadrat was used as the random intercept to account for data non-independence. This relationship would be coded in R as Cells occupied ~ Sward height * January temperature association + Sward height * July temperature association + (1 | Quadrat). The number of 10km cells occupied was subject to BoxCox transformation to achieve normality of residual distribution for this mixed model.

Results

Temperature Preferences

Species with relatively high January temperature associations occupied areas with significantly higher mean solar insolation coefficients ($F_{1,2203} = 14.441$, $p < 0.001$, $R^2 = 0.349$, Fig. 3a). Species with relatively high July temperature associations occupied areas with significantly higher mean solar insolation coefficients, and this relationship was increased in areas with shallower soil depth ($F_{1,3527} = 15.003$, $p < 0.001$, $R^2 = 0.268$; Fig. 3b). Figure 3a suggests that species associated with Boreal-montane and Boreo-temperate biomes (Boreal in Fig. 3), which have the lowest January temperature associations, were found in areas with the lowest mean solar coefficients. However, other species with relatively cool January temperature association, such as *Allium schoenoprasum*, occupied micro-sites with relatively high mean solar coefficients.

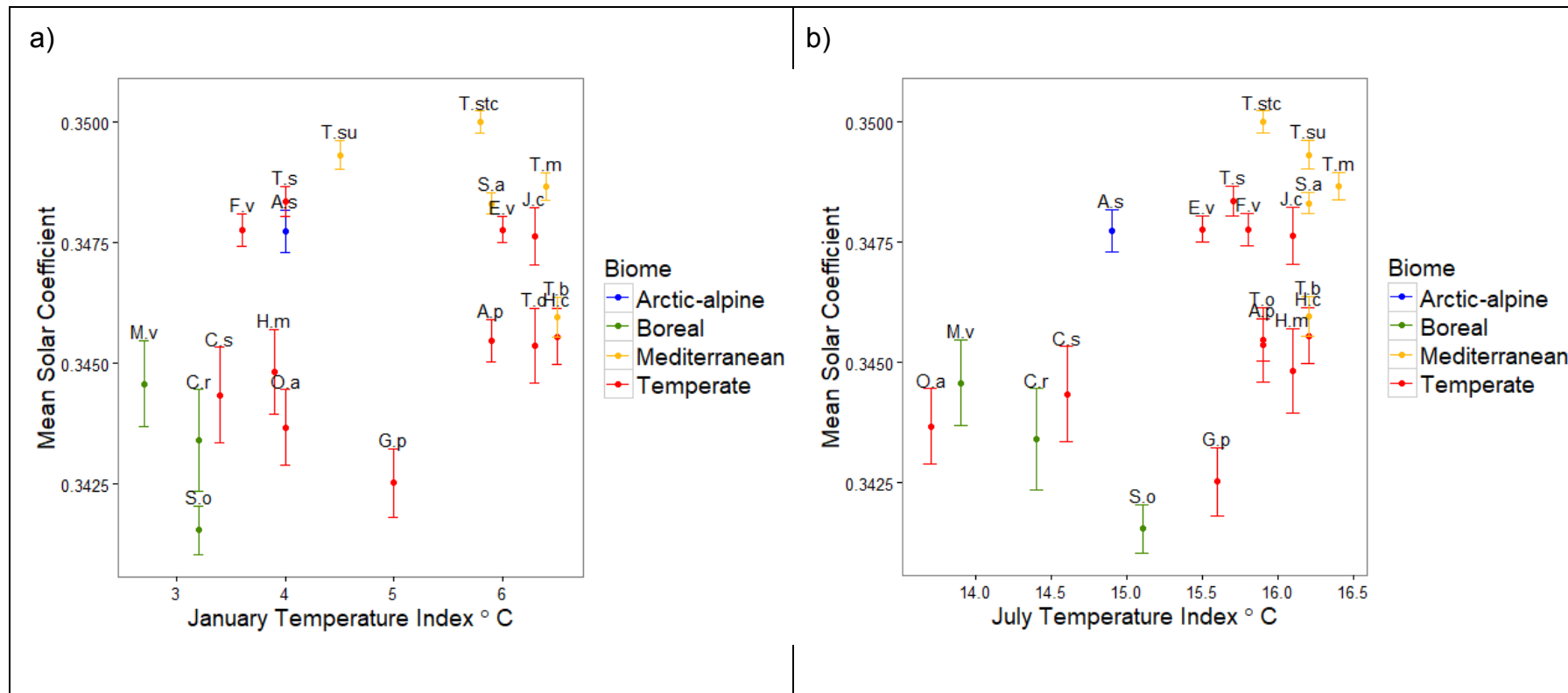


Figure 3. Relationship between microclimatic and macroclimatic temperature associations of selected plant species on the Lizard Peninsula, Cornwall. Microclimatic temperature associations are represented by the mean (\pm s.e.) proportion of direct beam irradiance received at locations in which each species was found across our study region (solar coefficient) and macroclimatic temperature associations by the mean January (a; $p < 0.001$, $R^2 = 0.349$) and July (b; $p < 0.001$, $R^2 = 0.268$) temperature of 10-km squares in Britain, Ireland and the Channel Islands in which each species was recorded in the New Atlas of British Flora (Hill et al. 2004). See Table 1 for species abbreviations.

Major biome

Species' major biome association was a significant indicator of the solar insolation coefficient of areas they occupied ($F_{5,13} = 3.339$, $p = 0.038$, $R^2 = 0.363$).

Species associated with the most northerly and southerly major biomes were found in areas with the highest solar coefficients (Fig. 4).

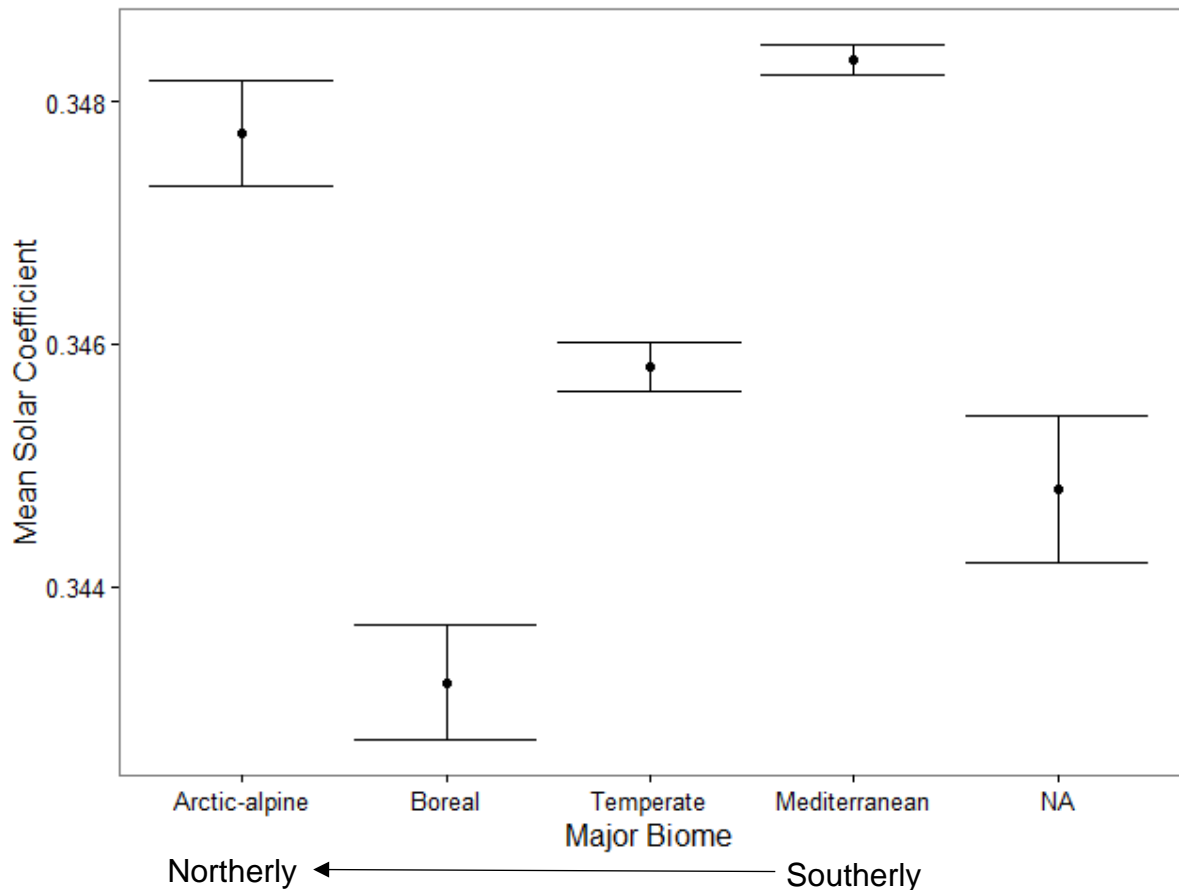


Figure 4. Relationship between microclimate temperature associations of selected species on the Lizard Peninsula and the major biome with which they are associated, where NA represents quadrats containing no target species ($p < 0.001$, $R^2 = 0.349$). Microclimatic temperature associations are represented by the mean (\pm s.e.) proportion of direct beam irradiance received at locations in which each species was found across our study region (solar coefficient). Major biome was based on Preston and Hill (1997), with Arctic-alpine being the most northerly biome classification in our study and Mediterranean the most southerly, see Table 1 for full details of species and biome classification.

Vegetation height

Species occupying more UK 10km cells were generally found in areas with significantly higher mean sward height and had warmer January and July temperature associations (January: $F_{1,3487} = 4.1$, $p = 0.042$, $R^2 = 0.699$; July: $F_{1,3538} = 26.9$, $p < 0.001$, $R^2 = 0.699$; Fig. 5).

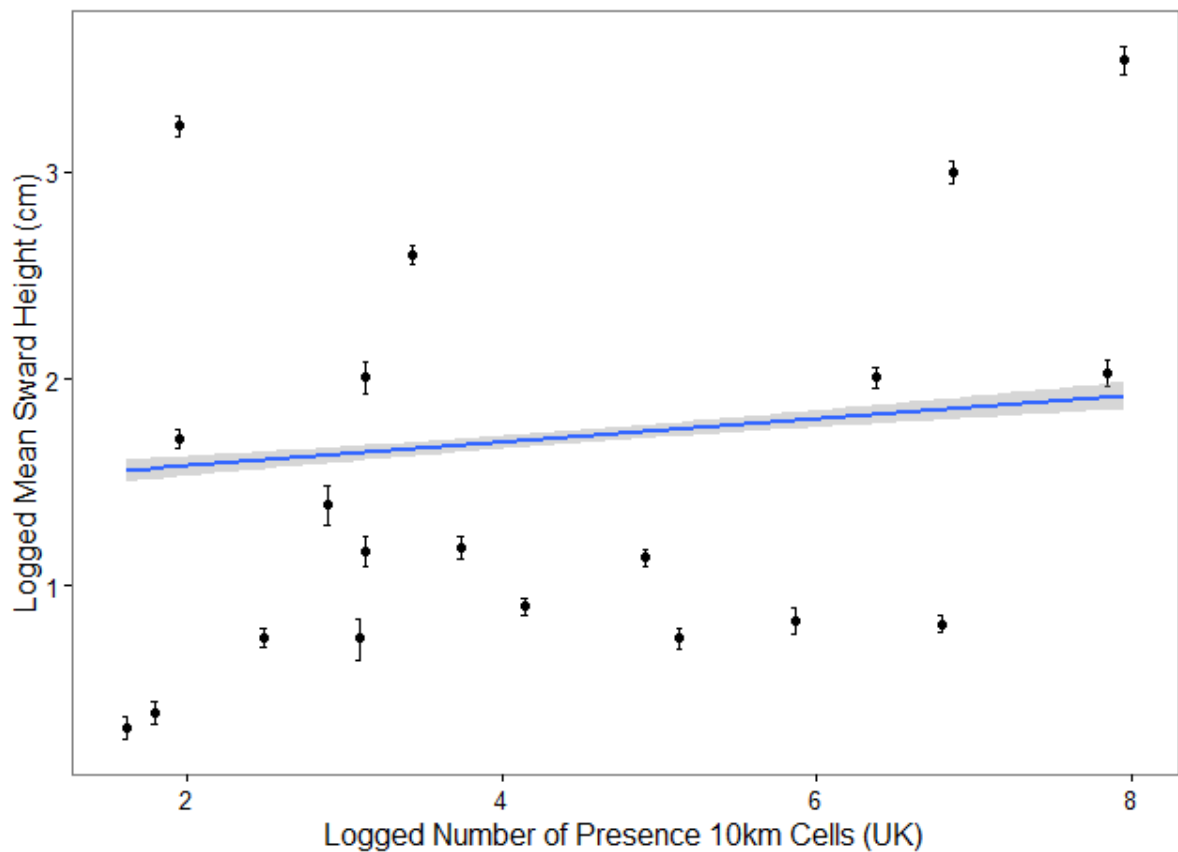


Figure 5. Relationship between the number of 10 km cells across the British Isles and the Channel Islands in which a species is present (Hill, Preston & Roy 2004) and mean (\pm s.e.) sward height of grid cells in which the species occurred on the Lizard Peninsula with the linear relationship shown, with standard error.

Discussion

My findings show that species distribution was influenced by differences in topography and sward height, both of which are indicative of variation in microclimate. I found that species from both the warmest and coolest major biomes occupy areas with the highest solar coefficient values, which experience relatively warm, dry microclimates. Further, I found rarer UK species typically occupy areas with the lowest sward height, which also have relatively warm, dry microclimates (Hill, Preston & Roy 2004).

To represent microclimate in our study, I used solar insolation as a proxy, as it plays an important role in determining near-surface temperatures, evaporative demand, and soil moisture of a site at the fine scale (Bennie *et al.* 2008; Maclean *et al.* 2017). Given the relatively narrow latitudinal range of my study site (49.9582°-50.0912°), slope and aspect are the main drivers of variation in insolation (Geiger 1965). I would expect solar insolation to be highest on steep, south-facing slopes. Although the positive relationship between solar insolation and local temperature is strong in clear sky conditions, no adjustment to solar insolation was made for cloud cover or for transmission through vegetation. Similarly, wind strength was unaccounted for, which also plays an important role in local climatic variation, with sheltered, south-facing slopes experiencing warmer temperatures than more exposed ones (Bennie *et al.* 2008). Despite excluding cloud cover and wind strength, it has been shown that solar insolation measured using topographic variation is the dominant influence for soil moisture and near-surface temperature variation at fine spatial scales (Bennie *et al.* 2008; Maclean *et al.* 2012, 2017).

My findings show there was a positive linear relationship between species' macroclimatic temperature preferences and the solar insolation of the areas species occupied. Species with the highest July temperature preferences are more likely to be found in areas with high insolation than species with low July macroclimatic temperature associations. This is except for *Allium schoenoprasum*, an Arctic-alpine species which occupies areas with higher solar insolation than would be expected from its macroclimatic preferences. Species from the Arctic-alpine and Mediterranean biomes occupy the areas with high insolation. This would be expected for Mediterranean species, however Arctic-alpine species on the Lizard would be expected to occupy the coolest microclimates, given their macroclimatic temperature preferences (Hill, Preston & Roy 2004).

I found rarer UK species typically occupy areas with the shortest sward. Areas with lower sward have higher microclimatic temperatures due to reduced shading from vegetation cover (Suggitt *et al.* 2011), and greater variation in moisture availability (Lin 2007). This is particularly interesting regarding rare species such as *Minuartia verna* and *Allium schoenoprasum*, which have cool macroclimatic temperature preferences, but occupy areas with the shortest sward. This suggests that reduced competition resulting from the higher temperatures and reduced moisture availability are a more important consideration for rarer species than macroclimatic associations. My findings suggest that species macroclimatic associations do not necessarily reflect their climatic tolerance. The reason species with cooler macroclimatic temperature profiles were found in areas with the highest insolation may be to do with moisture. The warmest sites are those with steep slopes and higher solar coefficients, which also experience greater

fluctuations in moisture availability (Penna *et al.* 2009). Species in areas that experience greater water fluctuations require traits that enable them to tolerate droughts. Many of these traits are found in species with cool macroclimatic temperature profiles, as the traits also enable plants to tolerate regular freeze/thaw conditions (Grime, Hodgson & Hunt 1988). Rapid development to a reproductive state when environmental conditions are favourable is one trait associated with freeze/thaw conditions. Arctic-alpine species are often adapted to freeze/thaw conditions, allowing them to take advantage of periods of high resource availability, and avoid resource consumption when other stressors are high. In consequence, Arctic-alpine species can achieve comparable levels of productivity to species in other biomes in less time as a result of their rapid development (Körner 2002). This enables Arctic-alpine species to take advantage of drought periods to reproduce, and so persist, when competition is reduced. A second trait that enables tolerance of both drought and freezing is photoinhibition, which allows a plant to limit the damage from excessive light energy when the energy is not being used for photosynthesis (Preston & Sandve 2013). This means that during drought, when photosynthesis is limited by water availability, the plant is better able to tolerate potential damage from excess light energy. The third trait plants subject to the stressors of drought or freeze/thaw exhibit is the ability to inhibit excessive hydraulic function toward susceptible or resource expensive organs, for example leaves and roots, in order to avoid damage or excessive resource consumption (Zanne *et al.* 2014). As a result, plants consume fewer resources in achieving growth during drought periods, and so can direct more resources to reproduction. These three traits to are so alike that it has been proposed that freezing tolerance arose from adaptations of drought tolerance mechanisms, due to the shared limitation of water deficiency

in both conditions (Guy 2003; Beck *et al.* 2007). The similarities in traits that underlie both drought and freeze/thaw tolerance might explain why Arctic-alpine species were found in the warmest microclimates. Arctic-alpine species' adaptation to freeze/thaw conditions predispose them to tolerate drought stress arising from water fluctuations on steep, south-facing slopes. Arctic-alpine plants therefore thrive on these slopes, which also have high solar coefficients and warm microclimates (Billings & Mooney 1968; Guy 2003). Many potential competitors are unable to occupy such habitats, and as such they have less competition than other slopes (Choler, Michalet & Callaway 2001). I therefore suggest that low competition resulting from drought-stress explains the confinement of Arctic-alpine species to warmer, south-facing slopes.

Many species with cool macroclimate associations occupied areas with short sward heights. However, rarer UK species with cool macroclimatic associations tend to be found in areas with shorter sward. It has been shown that there is greater fluctuation in temperature and moisture availability with reduced canopy shading (Lin 2007), leading to drought-like conditions. This suggests that drought-like conditions play a more important role in determining the distribution of rare species than does warm microclimates. This is further evidence that the distributions observed result from the ability of freeze/thaw adapted Arctic-alpine species to tolerate drought-like conditions (Guy 2003). The drought tolerance of the relatively rare Arctic-alpine species combined with the limited drought tolerance of other species provides Arctic-alpine species with a competitive edge in areas with short sward (Choler, Michalet & Callaway 2001; Liancourt, Callaway & Michalet 2005). If so, environmental fluctuations at a microclimatic scale would appear to be more important than macroclimatic temperatures in determining

Arctic-alpine species distributions on the Lizard. This is particularly important given that it is rarer species which appear to prefer areas with high insolation.

My findings show that the fine-resolution distribution of species with cool macroclimate associations differs from expected, likely because of the influence of microclimate. Thus, my findings contrast with previous suggestions that climate is unimportant at local scales (Pearson & Dawson 2003). This has important implications for the suitability of coarse-resolution SDMs in predicting species distributions, as the differences in microclimate resulting from topographic variability may not be represented by the mean climatic variable values used by coarse-scale SDMs (Franklin *et al.* 2013). Consequently, the available microclimatic niches that species can occupy cannot be included in coarse-scale models.

The availability of areas with a species' suitable microclimate is likely to vary between locations. Thus, if microclimate influences distributions, some species are more likely to be present in areas with greater availability of suitable microclimatic environments. In these areas, coarse-scale SDMs may underestimate available habitat with suitable climate for species. At the extreme, this could result in the presence of species in areas which, according to their macroclimatic associations, are predicted to be entirely unsuitable. Alternatively, the species macroclimatic associations calculated by coarse-scale models may overestimate the extent of suitable climate for species. This would occur if the microclimatic conditions a species occupied were only found in a small proportion of an area (usually a grid-cell) that is classed as occupied. The species' presence in this area would thus be associated with a macroclimatic temperature unrelated

to the climatic conditions it actually occupies. Both these scenarios would result in inaccurate predictions for species distributions. In particular, coarse-scale SDMs would misrepresent potential available habitat for species distributions in topographically diverse areas as a result of future change. Topographically diverse areas have the most spatial variation in microclimate, and so the greatest amount of information which cannot be included in a coarse-scale SDM. Misrepresentation of species distributions at the micro-scale does not necessarily invalidate coarse-scale SDMs, as unaccounted losses at the trailing edge due to generalised climatic conditions may be balanced by similar gains at the leading edge. However, if there is a bias in species persistence at the leading or trailing edge, coarse-scale SDMs are unlikely to be able to provide accurate representation of the direction of the bias. Previous studies show fine-scale SDMs can provide more accurate predictions for species persistence in topographically diverse areas due to microclimatic variation (Randin *et al.* 2009). That fine-scale microclimate influences species distribution suggests that it thus should be considered in SDMs to provide more accurate predictions of distribution changes.

At the location of my study site, my findings support the use of fine-scale SDMs in topographically diverse areas, as in this situation SDMs can identify suitable microclimates within the more broad-scale climate profile of an area. This allows fine-scale SDMs to predict potential species shifts across small spatial extents (Scherrer & Körner 2011) and avoid the potential for inaccurate predictions of local species persistence or extinction which may result from coarse-scale generalisation of climatic tolerance. However, I acknowledge that fine-scale SDMs are not suitable for all situations. In data-deficient regions fine-scale models may prove inaccurate due to lack of species distribution records (Moudrý

& Šimová 2012) or a paucity of fine-resolution environmental data. Consequently, coarse-scale SDMs may be more suitable for mobile species (Seo *et al.* 2009), which have a greater range and so experience a climate closer to that of macroclimatic conditions. Coarse-scale SDMs are also more suitable in homogenous landscapes, where they can accurately track climate change influence with less precise records over a wider area.

That my results highlight the importance of microclimate in determining species distribution has significant implications for conservation management. Two of the most prevalent management options presented as solutions to shifting distributions as a result of climate change are species translocation (Thomas 2011) and protected area networks (Araújo *et al.* 2011). While there have been successes (Molles *et al.* 2008; Gleason *et al.* 2010), both methods have significant drawbacks. The most important of these include financial cost (Beringer *et al.* 2002) and availability of suitable space (Liu *et al.* 2001; McRae *et al.* 2012). An alternative management method which is supported by my finding that microclimate influences species distribution is *in situ* landscape management. *In situ* landscape management can be used by managers to respond to the influences of climate change at a local scale, through manipulation of microclimatic conditions (Greenwood *et al.*, 2016). For example, increasing grazing to enhance small-scale heterogeneity in water availability for the benefit of ephemeral wetland species (Maclean *et al.* 2012; Scott *et al.* 2012). The main benefit of such management is that it can be used to promote species persistence in their current range in the face of climate change. This reduces the need for an increase in protected areas and may be used help to offset biodiversity loss in areas where species cannot otherwise be relocated.

In conclusion, I show that microclimate has an influence on species distributions at fine spatial scales. This has important implications for SDMs, as fine-scale SDMs may provide more accurate predictions for species distributions than coarse-scale models in topographically diverse areas. Coarse-scale SDMs generalise climatic conditions over a wider area than fine-scale SDMs. These climatic generalisations in topographically diverse areas may predict less microclimatic tolerance than the species have, and thus underestimate local suitable habitat. An example of this is in Arctic-alpine species, which I found occupy areas with the warmest microclimate, in direct contrast to their recorded preference for cool temperatures. This is an important finding for biodiversity conservation through predicted climate change. It suggests that current prediction methods may provide misleading evidence on which protected networks and species translocations are based, if coarse-scale models are used without thought. *In situ* landscape management may also offer a viable alternative, as it offers managers the ability to respond to the influences of climate change as they happen at a local scale, though in many areas the lack of empirical evidence limits the guidance managers are provided. Thus, I believe that fine-scale modelling of species' responses to climate change is imperative if we are to effectively manage global biodiversity in the face of climate change.

Chapter 4: Using *in situ* management to conserve biodiversity under climate change

Summary

1. Successful conservation will increasingly depend on our ability to help species cope with climate change. While there has been much attention on accommodating or assisting range shifts, less has been given to the alternative strategy of helping species survive climate change through *in situ* management.

2. Here we provide a synthesis of published evidence examining whether habitat management can be used to offset the adverse impacts on biodiversity of changes in temperature, water availability and sea-level rise. Our focus is on practical methods whereby the local environmental conditions experienced by organisms can be made more suitable.

3. Many studies suggest that manipulating vegetation structure can alter the temperature and moisture conditions experienced by organisms, and several demonstrate that these altered conditions benefit species as regional climatic conditions become unsuitable. The effects of topography on local climatic conditions are even better understood, but the alteration of topography as a climate adaptation tool is not ingrained in conservation practice. Trials of topographic alteration in the field should therefore be a priority for future research.

4. Coastal systems have the natural capacity to keep pace with climate change, but require sufficient sediment supplies and space for landward migration to do so. There is an extensive literature on managed realignment. While the underlying rationale is simple, successful implementation requires careful

consideration of elevation and past land use. Even with careful management, restored habitats may not attain the physical and biological attributes of natural habitats.

5. *Synthesis and applications.* The recent literature provides a compelling case that some of the adverse effects of climate change can be offset by appropriate management. However, much of the evidence for this is indirect and too few studies provide empirical tests of the long-term effectiveness of these management interventions. It is clear from the existing evidence that some techniques have a higher risk of failure or unexpected outcomes than others and managers will need to make careful choices about which to implement. We have assessed the strength of evidence of these approaches in order to demonstrate to conservation professionals the risks involved.

Key-words: adaptive management, biodiversity conservation, climate-change adaptation, environmental change, global warming, habitat restoration, managed realignment

Introduction

Over the next 100 years, climate change is likely to become one of the main drivers of biodiversity loss world-wide (Maclean & Wilson 2011). Conservation policymakers and practitioners thus face the challenge of enhancing the adaptive capacity of biodiversity to climate change (Heller & Zavaleta 2009). However, ecosystems have been modified extensively and it is likely that a substantial proportion of species will be hindered from tracking climate change by their inability to traverse large distances over hostile land cover (Mantyka-Pringle,

Martin & Rhodes 2012). Although numerous species have redistributed towards higher latitudes and elevations (Chen *et al.* 2011), for many the shift has not been fast enough to keep pace with climate change (Menéndez *et al.* 2006). While much discussion of adaptation to climate change has focussed on accommodating or assisting these range shifts, less attention has been given to the alternative strategy of improving species' ability to cope with climate change within their existing range. One means the conservation world has of achieving this is by manipulating habitat conditions to better match species requirements. However, to date, there has been little guidance from scientists about how this can be achieved.

Many species, particularly in Europe and North America, are reliant on habitat manipulation (e.g. Luoto, Pykälä & Kuussaari 2003). It has also been demonstrated that some species can alter their use of habitat in response to variation in climate, for example utilizing cooler habitats more frequently when temperatures are warmer (Suggitt *et al.* 2012). Taken together, these lines of evidence suggest that habitats can be manipulated to buffer species against the adverse effects of climate change. The evidence that such an approach may be effective, while indirect in many cases, is growing. Here we review this evidence. Temperature is not the only component of the climate that is changing, however. Changes in precipitation and, by extension, water availability may have even greater impacts on ecosystems than temperature and indirect impacts such as from sea-level rise will also be important (IPCC 2013). Our review thus focuses on terrestrial impacts and on three of the major environmental changes associated with climatic change: temperature, water availability and sea-level rise.

A wide spectrum of site-based approaches has been proposed to adapt conservation to climate change. However, many are generic, available to conservation managers irrespective of climate change. It is impractical to attempt to cover all techniques for site-based conservation in a single review, so our review of these wider techniques is limited to a brief synthesis. Our primary focus is on how *in situ* management could be used to manipulate the climatic conditions experienced by organisms. As our aim is to provide guidance for site managers, we also highlight a few instances where localized landscape management, such as catchment hydrology manipulation, could enhance the *in situ* persistence of target species.

Materials and methods

To identify potential management techniques, we searched Web of Science using terms related to climate change and management (see Appendix S1 in Supporting Information for list), identifying 101 studies as potentially relevant. Each of these was studied and the reference list queried to identify further relevant studies. Any additional studies known to the authors were also included. Our review is based on information in 67 relevant papers identified in this way. Full details of the search methods are provided in Appendix S1.

The strength of evidence for each management technique was assigned a quantitative score using three criteria: (i) the magnitude of the responses reported by each study; (ii) the overall confidence in the documented responses and (iii) the number of studies reporting that management technique. The risk of failure associated with each management technique, both in terms of the risk that the

technique is ineffective and in terms of undesirable side effects, was assigned a quantitative score using: (i) the likelihood of an adverse response (assessed using the confidence in reported responses) and (ii) evidence in the wider literature not pertaining to climate change that such management can have undesirable effects. Economic feasibility was not considered. Formal definitions and the methods by which scores were combined are provided in Appendix S1. A full list of potential management techniques is provided in Table 1. Those that have been shown to be consistently ineffective are shown in Table 2.

Management to offset the effects of temperature change

Mean temperatures and the frequency of extreme warm temperature events are both predicted to increase by 2100 (IPCC 2013), with two important implications for wildlife: (i) populations or individuals that fail to track their thermal niche could suffer a reduction in fitness, leaving them more vulnerable to other stressors and (ii) the increasing regularity of extreme events will give populations less time to recover from shocks (Oliver, Brereton & Roy 2013). The principal means of offsetting warming involve manipulation of vegetation and/or topography. Differences in vegetation type and height are well-established modifiers of the thermal environment. Local temperatures in areas with less vegetation cover are generally cooler during the night and warmer during the day (Suggitt *et al.* 2011) and several studies, particularly on thermophilous insects, demonstrate the importance of these variations in microclimate in determining distribution and abundance (Thomas 1993). For example, for the Glanville fritillary butterfly, the availability of suitable microclimates (as determined by the successional stage of vegetation) is almost twice as strong a predictor of butterfly abundance as regional air temperature (Curtis & Isaac 2015), probably because species can

change habitat association in response to ambient temperatures (Suggitt *et al.* 2012). Given that species may shift into relatively cooler habitats in response to warmer temperatures, it would appear axiomatic for land managers to implement management that results in more vegetation cover. However, given that loss of early-successional habitat has been linked to species declines (e.g. Thomas *et al.* 2004) and that such habitats can be cooler at night, the creation (and maintenance) of thermally diverse habitats remains the current priority in insect conservation (Thomas, Simcox & Hovestadt 2011). Although there is less evidence for taxa other than butterflies, it has been suggested that the thermal properties of microsites influence the distribution of a variety of other taxa (e.g. Kearney *et al.* 2007; Barnagaud *et al.* 2013).

In aquatic ecosystems, where fluctuations in temperature are dampened by the higher specific heat capacity of water, a number of studies indicate that the maintenance of riparian shade can reduce temperatures sufficiently to offset the effects of climate change. For example, Broadmeadow *et al.* (2011) demonstrated that even relatively low levels of shade (20–40%) can be effective in keeping summer temperatures below the incipient lethal limit for brown trout, *Salmo trutta* L., although c. 80% shade would be needed to prevent temperatures exceeding those for optimal growth. While the evidence relates to salmonoid fish in cold-water streams, there is growing evidence from a broader range of systems (e.g. Mantyka-Pringle *et al.* 2014; Table 1). Additionally, riparian shading management may also increase bank stability and reduce sediment transport and/or erosion (Pawson *et al.* 2013). This practice is the subject of an increasing number of focussed initiatives world-wide (Britain, Lenane 2012; California, Stein *et al.* 2013). Other actions to improve water availability in aquatic ecosystems

(e.g. artificial wetting; Mitchell 2001) are also likely to reduce the effects of extreme heat. Topography, particularly the aspect and angle of slopes, controls the amount of radiation received near the Earth's surface and hence exerts strong influences on the temperatures experienced by many organisms, particularly in mid-latitudes to high latitudes (Table 1). As with vegetation structure, there is much evidence that local variation topography interacts with regional climate to have major influences on species distribution and abundance. For example, many species are restricted to warmer, equatorward slopes at their poleward (cold) range margin (Pigott 1968). Increasing evidence also demonstrates that variations in topographic microclimate can also buffer the effects of climate change (Suggitt *et al.* 2014, 2015; Maclean *et al.* 2015). While the potential to alter topography through management is not well ingrained in conservation practice, there have been notable successes (Table 1). For example, work to restore quarries after mineral extraction (Nature After Minerals 2015), and more specifically the creation of artificial scrapes (e.g. Slater 2014) have been shown to benefit both butterflies and plants. Furthermore, many housing and infrastructure development projects entail the artificial profiling of construction sites, which in some cases has led to successful colonizations of sites previously unimportant for wildlife (e.g. Danahar 2011). Increasingly, developers are required to mitigate or offset the ecological impacts of construction through the creation or restoration of habitats for wildlife (Defra 2013). It is easy to envisage a process whereby topographic variation is deliberately enhanced as part of such activities.

Given the effort and likely expense associated with altering topography or manipulating vegetation, the current advice to land managers remains that the

creation of thermally diverse areas can be beneficial in that it can promote population stability, ameliorate the higher and more variable temperatures associated with climate change and is likely to provide habitat for a wider variety of species (Macgregor & van Dijk 2014; Table 1). However, many sites are managed specifically for single species or related species reliant on specific habitat or topographic requirements. In these instances, the creation of more heterogeneous environments would be undesirable if at the expense of reducing the amount of optimal habitat. For example, within the UK, maximizing the availability of warm microclimates could benefit one-sixth of rarer British butterfly species (Thomas 1993), but this creation of warm microclimates may be detrimental to the remainder. The trade-off between maintaining species diversity and increasing (general) abundance remains complex and reinforces that research at greater spatial and ecological detail remains a priority to understand the impact of climate change (Kearney & Porter 2009).

Table 1. Management responses to climate change, with associated effects on the environment and on wildlife. For each response, the strength of supporting evidence and risk of failure is also assessed. Separate assessments for each study are provided in Table S3. Superscript numbers cross-reference with those in Appendix S2, in which further details are provided.

Adverse effect	Management technique	Positive effects on wildlife	Potential adverse effects on wildlife	Strength of evidence	Risk of failure
Warming	Afforestation ¹⁻³ and abandonment/reduced grazing ⁴	Increased/denser vegetation cover reduces maximum temperatures and buffers species against temperature extremes, but may have undesirable effects on non-target species.	Increased resource competition.	Moderate/Strong	Medium
	Slope creation/ protection ⁵⁻⁷	Equatorward-facing slopes accommodate range expanding species; Poleward-facing slopes benefit range retracting species. Topographic heterogeneity buffers species against adverse effects of climate.	Reduced availability of optimal habitat.	Strong	Medium

	Woody debris addition ⁸	Stabilises soil temperature and reduces moisture loss benefiting species with high moisture and low temperature requirements.	Reduced light availability	Low	Medium
Precipitation change	Altering grazing regimes ^{9,10}	Livestock exclusion counteracts hydrological effects of increased winter precipitation in California with benefits to plants, amphibians and invertebrates. Increased grazing reduces infiltration and enhancing small-scale heterogeneity in hydrological conditions, benefiting ephemeral wetland species in the UK. High risk of failure as grazing can have both positive and negative impacts.	Reduced grazing may reduce diversity, particularly in areas with productive soils and high rainfall.	Moderate	High
	Manipulate water flow with permeable ¹¹ or	Permeable barriers regulate water flow and create shallow pools. Biological benefits untested. Drain blocking enhances key peatland	Unknown	Moderate	Low

	impermeable barriers ¹² , or drainage control ^{12,13}	species. Diverting ditches improves conditions for wet grassland birds.			
	Irrigation/spraying ¹⁴	Increases water availability; enhanced amphibian spawning. Expensive.	Reduced water availability elsewhere.	Strong	Medium
Sea-level rise	Sea-defence creation/maintenance ¹⁵⁻¹⁹	Protects coastal habitats from seawater intrusion. Benefits non-marine species or those with specific salinity/water requirements. Creation of textured surfaces and artificial rockpools create habitat for intertidal organisms. Options for soft-engineering oyster and mussel beds as offshore barriers. Stabilisation/accretion of material on sandy beaches.	Altered sediment transport may increase erosion offsite.	Strong	Medium
	Stabilisation of intertidal and coastal habitat ^{20,21}	Sediment addition to intertidal habitat increased surface elevation offsetting sea-level effects with	Cord-grass highly invasive, potentially	Strong	Medium

		benefits to intertidal communities. Planting / protection of e.g. cord-grass or marram grass stabilises coastal habitats.	reducing native biodiversity		
	Defence realignment ²²⁻²⁴	Intertidal habitat creation. Benefits to waders, saltmarsh plants and benthic invertebrates.	Adverse effects unlikely, but benefit depend on shore profile and morphology.	Moderate	Medium
	Active management of newly created habitat, including seeding ²⁵ , re-profiling and sediment addition ²⁶	Ensures newly created intertidal habitat more similar to natural habitat. Increased diversity of benthic invertebrates and saltmarsh plants.	Reduces suitability of wader feeding habitat (exposed mud).	Moderate	Low

Table 2. Potential management responses to climate change, which have been shown not to work. Superscript numbers cross-reference with those in Appendix S3, in which further details are provided.

Adverse effect	Management technique
Warming	Adding fertilizer to promote vegetation growth ¹
Precipitation change	Keeping rice fields flooded after harvest ²
	Rewetting soils in old arable fields ³
Sea-level rise	Raising areas of substrate for nesting birds ⁴

Management to offset the effects of water availability change

Globally, trends in precipitation are not clear-cut (IPCC 2013) and environmental managers are likely to be faced with the challenge of adapting nature conservation to both wetter and drier conditions, sometimes in the same location at different times of year. Notwithstanding this challenge, there is a substantial precedent in managing landscapes to regulate water supply (Table 1), reduce flood risk (O'Connell *et al.* 2007) and manage water levels to enhance biodiversity (Eglington *et al.* 2010), and thus, there is considerable potential to offset the effects of climatic change on water availability through habitat management.

Broadly, three management approaches have been used to influence water availability (Table 1), although many examples are not specifically associated with adapting nature conservation to climate change. The first entails modifying land use to divert or regulate water supply downstream. In grazing marshes in the East of England for example, artificial shallow drains have been used to divert water to the middle of marshes. This process creates areas of flooding and damp habitat that can potentially provide a mosaic of nesting habitat and profitable feeding areas for breeding waders (Eglington *et al.* 2010). Similarly, Mitchell (2001) manipulated water availability at breeding sites for brown toadlet, *Pseudophryne bibronii* Günther, in South Australia using portable irrigation sprayers, with improvements in breeding success. The small spatial scale at which most amphibians operate makes them ideally suited to habitat manipulations of this type and there is consequently considerable potential to offset some of the adverse effects of climate change on amphibians through active management (Table 1).

A second approach involves manipulating catchment hydrology to influence water availability upstream. For example, the soil moisture of peatlands in the United Kingdom has been manipulated by blocking ditches. This in turn increases cranefly *Tipulidae* abundance, particularly in dry years (Table 1). Craneflies are a key herbivore in these habitats and an important prey item for breeding birds, but they are susceptible to drought. The diversion of water (partly to benefit wildlife) can, on occasion, operate on a grand scale. In Florida, for example, there are plans to construct canals and levees to restore the everglades over an area of 47 000 km² (RECOVER 2014).

Lastly, habitat management can be used to manipulate vegetation structure, which in turn influences hydrology by affecting evapotranspiration. For example, Pyke & Marty (2005) showed that cattle grazing offsets the effects of increased winter precipitation on the hydroperiod of ephemeral wetlands by enhancing evapotranspiration, thus improving conditions for endangered invertebrates and amphibians. However, cattle grazing can also have the opposite effect. The depressions created by livestock trampling often accumulate water, and in some instances grazing is used as a means of ensuring conditions remain suitably wet (Maclean *et al.* 2012; Scott *et al.* 2012). Thus, the effects of grazing on hydrological conditions are not necessarily predictable and site-level knowledge or experimentation may be essential for successful conservation outcomes.

This latter finding serves to illustrate one of the challenges faced by managers: namely what to do when. Arguably the most important consideration will be what changes are expected. Where reductions in water availability are forecasted, creating wetter conditions is likely to be beneficial and vice versa. Where greater

variability is predicted, the creation of a stable water supply is likely to be desirable. A means of achieving greater stability is through the creation of permeable timber barriers, artificial diversion ponds and careful positioning of woody debris in streams, all techniques which have been used to attenuate run-off during periods of high rainfall (Table 1). Where there is uncertainty surrounding the availability of water, techniques that enhance heterogeneity in water availability are likely to be the most effective as they will increase the likelihood that suitable conditions for target species exist. Management techniques for achieving this include the creation of shallow scrapes and pools using heavy construction plant machinery (Natural England 2010) or encouraging low-density livestock grazing and trampling in marshes, fens and wet meadows (Tesauro & Ehrenfeld 2007). Bunding ditches (or diverting them to increase drainage in areas where susceptible to undesirable flooding) should also be considered as interventions in wet grassland, peatland and mire systems (Hopkins *et al.* 2007). It should be noted, however, that grazing can also have adverse effects in some ecosystems, particularly drier systems, or fail to have desired benefits (Lunt, Jansen & Binns 2012) and increasing heterogeneity may reduce the availability of optimal habitat. Any changes in grazing regimes or other management techniques implemented to increase heterogeneity should thus proceed with caution.

Management to offset the effects of sea-level rise

Global sea levels rose by approximately 0.19 m between 1901 and 2010 (Hay *et al.* 2015) with predicted rises of 0.25–1 m over the 21st century (IPCC 2013). Rising sea levels affect the extent and quality of coastal habitats through erosion and changes in niche availability and increase the vulnerability of inland habitats

to seawater flooding. There are particular problems where coastal development and construction of hard defences prevent landward migration of habitats, resulting in them being squeezed between a fixed landward boundary and rising sea levels (Morris *et al.* 2004). While this review deals with *in situ* management in response to these threats, it is worth emphasizing that such management should sit alongside landscape approaches, because even modest coastal development can alter natural coastal dynamics over hundreds of kilometres (Hapke, Kratzmann & Himmelstoss 2013).

Appropriate *in situ* management to offset the effects of sea-level rise depends mainly on the habitat type in question. Freshwater and brackish habitats, such as saline lagoons, require protection from tidal inundation because species are vulnerable to increases in salinity, which can lead to shifts in community composition (Tate & Battaglia 2013). Where landward retreat of these habitats is not possible due to adjacent land use, protection from saline flooding by the maintenance of hard or natural defences (e.g. sand or shingle barriers) is likely to be most effective. For example, sea walls at RSPB Titchwell, Norfolk, UK, were replaced or strengthened to protect important freshwater habitats, as part of a package of measures aimed at adapting the reserve to rising sea levels (RSPB 2013). Given the conservation value of these specialist communities (Beer & Joyce 2013) and their vulnerability to sea-level rise (Spencer & Brooks 2012), investment to maintain defences may be justified.

Rocky intertidal habitats are among the most vulnerable to rises in sea level because many are backed by steep inclines (such as hard cliffs) and are thus

unable to retreat landward (Jackson & McIlvenny 2011). Two forms of management are likely to be particularly effective. First, the creation of hard and rock-armoured defences, such as breakwaters, gabions and offshore barriers, can be used to absorb wave energy and reduce local erosion (French 2001) and are colonized by intertidal organisms. However, intertidal communities on existing hard defences are less diverse than those on natural rocky shores because the defences lack environmental heterogeneity, tending to be smooth and steeply grading (Table 1). Creation of microhabitat features (e.g. shaded vertical surfaces and water retaining features that mimic rock pools) increases the diversity of algal and macrobenthos communities and increases the potential for artificial barriers to compensate for loss of existing rocky intertidal habitat (Table 1). An alternative approach is to promote ecologically engineered offshore barriers, such as those created by reef-building oysters and mussels (Borsje *et al.* 2011). These can attenuate wave energy and stabilize intertidal flats behind them, although their effectiveness may be limited in high-energy environments (Table 1). Oyster reefs have declined by 85% over the past 100 years (Beck *et al.* 2011), and the creation of ecologically engineered reefs has the dual benefit of increasing habitat extent and providing a self-sustaining barrier that can keep pace with sea-level rise (Rodriguez *et al.* 2014). The decision as to which type of barrier to create depends on whether the goal is to create a specialist ecological community (ecologically engineered reef), or provide suitable habitat for a wider algal and macrobenthos community (artificial barriers).

Soft-sediment intertidal habitats are able to accrete vertically and maintain their elevation with respect to rising sea levels if there is a sufficient supply of sediment and conditions are suitable for settlement (Krauss *et al.* 2014). Structures such

as groynes and brushwood fences have been used to interrupt the movement of sediment and encourage local deposition, therefore increasing habitat extent by widening beaches (Table 1). However, if insufficient sediment is available to maintain habitat extent, additional material can be added to the system. For example, material from dredged sites can be added to beaches or eroding saltmarshes to increase the width and/or surface elevation, which may have the added benefit of increasing plant above-ground biomass, which in turn can stabilize the saltmarsh surface (Table 1). The source of the sediment for such nourishment schemes is an important factor. Fine-grained material is more likely to be resuspended and washed away and the form of benthic invertebrate communities is highly dependent on the grain size of the added material (Bolam & Whomersley 2005; Table 1).

Creation of new coastal habitats adjacent to existing ones is likely to be the most effective long-term option. Managed realignment, where sea defences are relocated landward and the old, seaward defences are breached to allow tidal inundation (French 2006), is the most commonly used method to create intertidal flats and saltmarshes. While not strictly *in situ* management, it often falls within the remit of a site manager to consider such an option and we therefore provide a brief overview of its efficacy. The most important factor in the success of these schemes is the surface elevation of the site, since this determines the colonization and subsequent composition of communities. Most sites selected for managed realignment are low-lying with respect to sea level (Crooks *et al.* 2002). This maximizes the length of time the habitat remains unvegetated and thus suitable feeding habitat for wading birds (Table 1), but is not desirable if the aim is to quickly establish vegetated saltmarsh (Garbutt *et al.* 2006). While benthic

infaunal and saltmarsh plant species can often colonize quickly (Mossman *et al.* 2012), natural communities can be more difficult to recreate (Mossman, Davy & Grant 2012). Artificial planting of rare species accelerates vegetation development, and may be particularly beneficial if the plant species host rare invertebrates (Woodell & Dale 1993). Plant colonization may be constrained by poorly drained and oxygenated sediments (Mossman, Davy & Grant 2012), which may be improved by the establishment of effective creek networks (Crooks *et al.* 2002) or the creation of more varied topography through constructing raised and lowered areas (Table 1). The grazing of saltmarshes can also generate habitat heterogeneity and may be particularly desirable when vegetation is dominated by invasive high-marsh grasses (Bos *et al.* 2002). In these situations, extensive grazing can increase plant diversity and create habitat more suitable for waterfowl, potentially mitigating for some sea-level induced impacts (Clausen, Stjernholm & Clausen 2013).

General *in situ* management techniques

In addition to manipulating environmental conditions, there are several more general methods that have been used to enhance the capacity for biodiversity to cope with climate change (see, e.g., Macgregor & van Dijk 2014). At the most generic level this may simply involve reducing other threats. The general contention is that, by reducing or preventing other threats to biota, target wildlife is better able to cope with climate change. Although it can be assumed that ameliorating the risk from these other threats will benefit a species' climate response, direct evidence of this occurring in practice has been more forthcoming for some threats than others. Interactions with pest species have been particularly well documented and there is a substantial amount of evidence that exposure to

pest species makes affected species more vulnerable to drought-induced water stress (Breshears *et al.* 2005), while also impeding the recovery of forests from extreme storm events (Pawson *et al.* 2013). The compounding effects of species invasions and climate change are also well documented, but most of the evidence for the utility of this approach is mixed and context-dependent, primarily because the evidence for competition-related declines is similarly conflicting. In the UK for example, 'non-native' plants have limited negative impact on native diversity (Thomas & Palmer 2015), but in the Alps, high-altitude plants are being out-competed by low-altitude plants (Gottfried *et al.* 2012), and here the lack of an alternative habitat (upslope) strengthens the case for interventions to defend what climatically suitable habitat remains. The realities of conservation funding mean that attention in this area is focussed on those species with the highest economic impact, and thus, evidence we have for the efficacy of invasion control is similarly biased. However, there are cases where the increased prevalence of 'non-native' species interacts with climatic conditions to compound the adverse effects. For example, vigorous, competitive invaders such as *Rhododendron ponticum* are likely to reduce understorey microclimatic heterogeneity and floating Cyanobacteria can lead to the loss of cold-water refugia as a result of hypolimnetic anoxia (Havens 2008).

The maintenance of genetic, species or functional diversity within ecosystems (see Folke *et al.* 2004 for a detailed review), has also been advocated, primarily for the purpose of bet-hedging: more diverse systems are better positioned to withstand climate change. For example, the effects of extreme drought on plant communities are patchy, affecting some species more than others (Buckland *et al.* 1997). Consequently, maintaining the diversity of these plant communities 'bet

hedges' that those species that are more tolerant or resistant to drought will be conserved (Díaz & Cabido 2001). The same principle has also been proposed at the genetic level, where populations with more genetic diversity are often found to be more resistant or resilient to extreme climatic events (Jump & Peñuelas 2005). While the general applicability of the 'maintaining diversity' approach is at least partially supported by evidence that management to improve diversity in one particular taxon or group often benefits diversity in other groups (Maskell *et al.* 2013), the underlying rationale is at best equivocal. One of the key reasons why increased diversity has been suggested to increase resilience is based on the concept of functional redundancy: more diverse ecosystems are assumed to be better able to maintain function even when some species are lost. Nonetheless, even in diverse systems, the loss of a single species can lead to major changes in ecosystem function (Díaz & Cabido 2001). The opposing side of this argument is that protecting the natural function of ecosystems, species and communities will enhance their capacity to cope with climate change. These processes can be biological (e.g. pollination, dispersal, succession of vegetation) or physical (e.g. erosion and deposition, river migration). A good example of the benefits of maintaining natural processes is the managed realignment of coasts already discussed. However, the approach has been applied more widely and often has multiple benefits. The retention of deadwood and/or debris in forests, for example, both improves the diversity of saproxylic invertebrates (Pawson *et al.* 2013) and offers greater diversity of microhabitats for other potential occupants (Hobson & Mickleburgh 2008). This serves to illustrate a more general point: some (e.g. Bellard *et al.* 2012) have argued that our current knowledge of the impacts of climate change is highly disparate and uncertain. In such situations, 'no regrets' techniques are likely to be the most sensible to adopt.

Conclusions

The threats of climate change to biodiversity are driving changes in recommended conservation practice. However, the majority of recommendations thus far focus on the broader landscape level, for example by enhancing connectivity or increasing the number or size of reserves (Heller & Zavaleta 2009). Surprisingly, despite the extent to which current conservation management practice alters local environmental conditions, the use of management as a tool for manipulating these conditions has rarely been recommended as a means of helping species cope with climate change, except as a means of countering sea-level rise.

While empirical evidence for the effects on biota of these management actions is in its early stages, it is clear from the evidence already available that, in some circumstances, there is a compelling case for management. Nonetheless, some techniques have a higher risk of failure or unexpected outcomes than others. We have assessed the strength of evidence of a selection of the approaches (Table 1) in order to provide an indicative idea to conservation professionals of the likely effectiveness of a given approach. We also assess the risk of failure, as some techniques may have undesirable effects and provide a list of those techniques that are unlikely to work (Table 2). There will also be inherent trade-offs: for example, prioritizing heterogeneity will come at the expense of some 'optimal' habitat for species. Allowing taller vegetation to establish will reduce light availability and provide a higher degree of competition (WallisDeVries & Van Swaay 2006). The degree to which one strategy or another is preferable will also depend on the time period over which it is enacted, with techniques to protect

existing biota at a site more attractive in the short term, but accommodation or even encouragement of change likely to be required in the long term (Rannow *et al.* 2014).

Overall, however, replicated and monitored local manipulations of habitat that ascertain the efficacy of management actions are rather scarce. Perhaps one of the reasons why such case studies are lacking is the weak implementation of adaptive management (e.g. Mitchell *et al.* 2007). In a technical sense, this entails manipulating a system to improve understanding and hence manage it more effectively. It is intended to be a structured, iterative process that leads to robust decisions in the face of uncertainty. In reality, however, it is often taken to mean that managers retain flexibility and respond as situations develop (e.g. Mitchell *et al.* 2007) and some argue that the phrase ‘adaptive management’ is usually used to disguise weak conservation practices (e.g. Sutherland 2006). Furthermore, even if applied correctly, the approach relies on there being measurable ecological responses to management that can be distinguished from other factors (Oliver & Morecroft 2014). Consequently, irrespective of whether management is being carried out adaptively or proactively, there is much need for well documented examples of habitat manipulations carried out in ways that permit their effectiveness to be established. It is thus important to document failure as well as success. It is likely that future efforts to safeguard biodiversity against the effects of climate change will require a rich variety of approaches. It is our belief that the deliberate manipulation of environmental conditions through habitat management should be considered as part of the suite of options available and the effectiveness of such actions adequately tested and documented.

Chapter 5: Conclusion

This thesis investigates the potential changes in species distributions in the face of climate change, the role climate at 1 km and 5m plays in these changes, and the conservation management options available to manipulate microclimate to conserve biodiversity. Chapter 2 finds that there has been significant environmental change on the Lizard Peninsula due to climate change over a comparable period, which is reflected in the plant community at a 1km scale. The changes observed in environmental factors suggest biodiversity loss is likely in the future without intervention. Chapter 3 provides evidence that microclimatic conditions influence species presence at the very fine scale (5m). This influence doesn't necessarily relate to species recorded macroclimatic preferences either. For example, both Arctic-alpine species, which have the coolest temperature preferences, and Mediterranean species, which have the warmest temperature preferences, were both found in areas with the highest solar insolation. Consequently, it may be that species predicted to become locally extinct may be able to persist in microclimatic holdouts, at least in the short term. Chapter 4 finds that the use of *in situ* management can be used to offset climate change locally, thus it may be that conservation efforts could be focused in key areas to conserve biodiversity. Efforts could be focused in areas where we might expect a diverse array of microclimatic conditions, such as topographically heterogeneous regions, or those with a patchwork of dominant land covers.

Future directions

This thesis identifies three key areas which would benefit from further investigation, namely; (i) increased species recording to improve understanding

of how environmental change due to climate change is affecting species distributions, (ii) more widespread use of fine-scale SDMs to predict changes in species distributions in topographically diverse regions and (iii) effective *in situ* management techniques, and their associated risks.

Chapter 3 evidences that microclimate may influence species distributions. Therefore, coarse-scale SDMs are unlikely to provide accurate predictions for species distributions in topographically diverse areas, as they cannot account for microclimatic variation. However, there are few studies which compare the accuracy of coarse-scale and fine-scale SDM predictions. I argue further investigation in to the effectiveness of different scale models is worthwhile. If conducted, a better understanding of how climate change influences species distributions at different scales will develop. Knowing when it is best to apply which type of model to determine species response will result in more accurate, less costly predictions.

To best make use of the available management techniques requires an accurate, long-term record of species distributions. With a greater availability of species records, we could investigate the environmental and community changes occurring over a comparable period. This would enable us to determine the effect climate change is having on global biodiversity. With this information, conservation managers could better direct their efforts, conserving more biodiversity with less expenditure. This is particularly important for understudied areas which are also biodiversity hotspots, such as the tropics. The tropics suffer

from a lack of knowledge of their current state, as well as a lack of guidance on how best to manage them.

One critical aspect of biodiversity management research is the lack of reporting of ineffective or harmful methods. The nature of journal publication is such that it is rare for a study finding no result, or an undesirable one, to be accepted. The consequence of this is that conservation managers are not made aware of which techniques have already been tried and failed. This leads to more resources being used ineffectually, or even be a negative impact on local biodiversity. Lack of information is particularly apparent for regions outside of North America and Europe. Thus, I argue that to improve the usefulness of *in situ* management, there need to be more studies reporting the effectiveness of management techniques over a wider region.

Conclusion

In conclusion, this thesis shows that scale of data is an important consideration when predicting species response to climate change. My findings suggest that changes in species distribution occur at a fine scale, raising issues with coarse-scale SDMs. As fine-scale variation in climate influence species response to climate change, *in situ* management can be an effective method for biodiversity conservation management through microclimate manipulation.

Appendix

Chapter 2

Figure S2.1

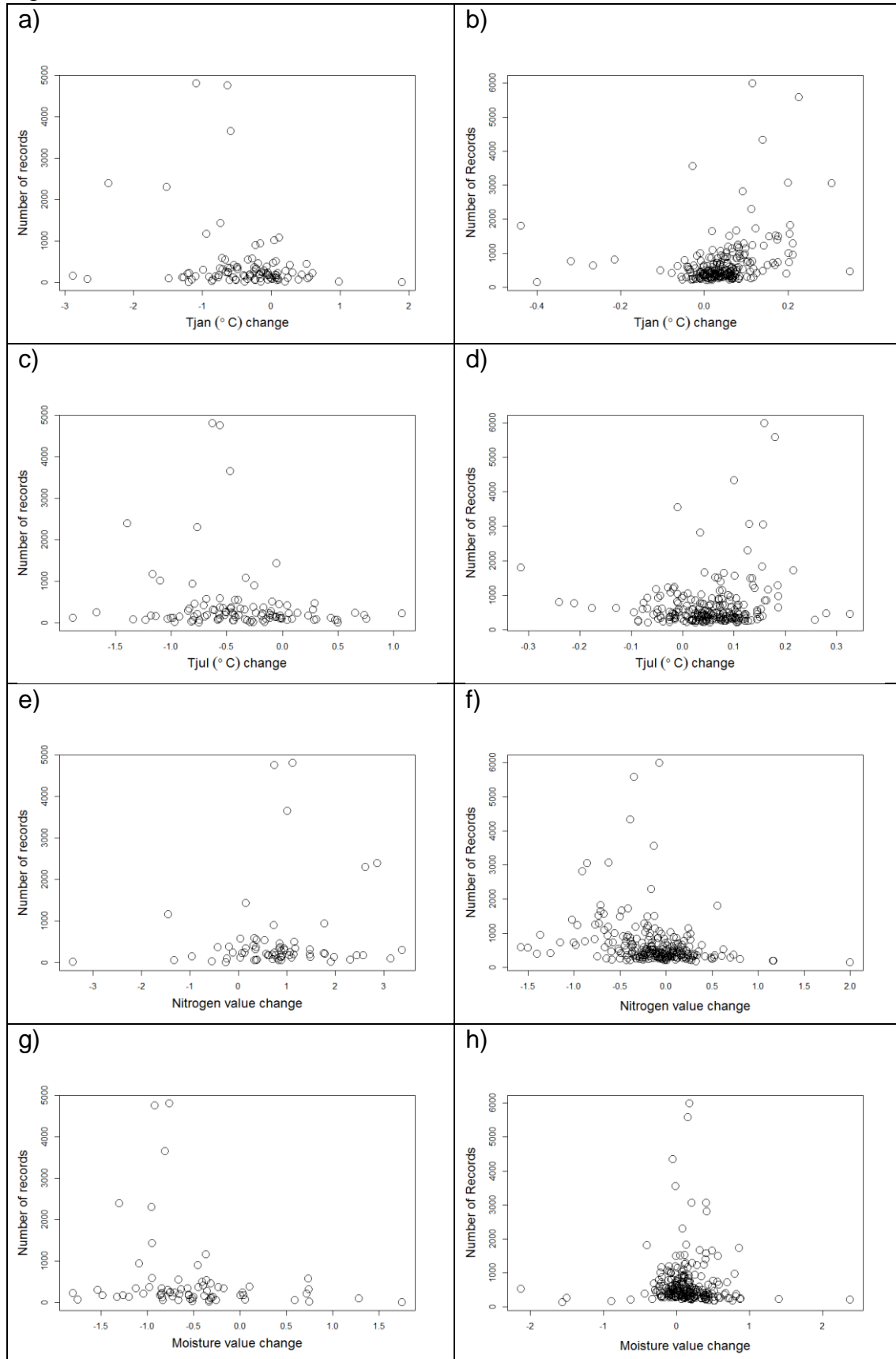
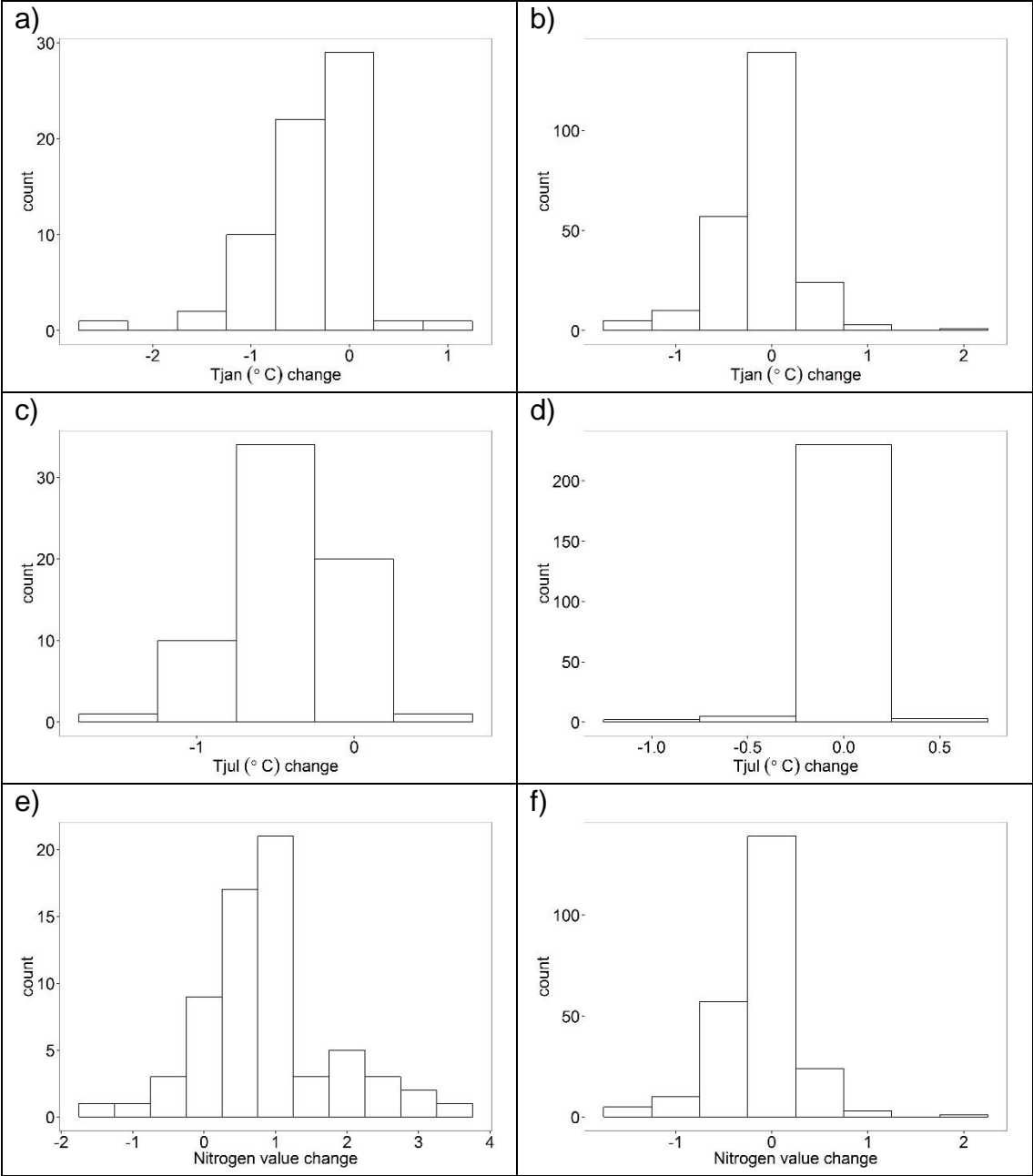


Figure S2.1. Funnel plots of the changes in mean indicator values between

periods one and two, and two and three against number of records for January temperature indicator values (a-b), July temperature indicator values (c-d), nitrogen indicator values (e-f) and moisture indicator values (g-h).

Figure S2.2



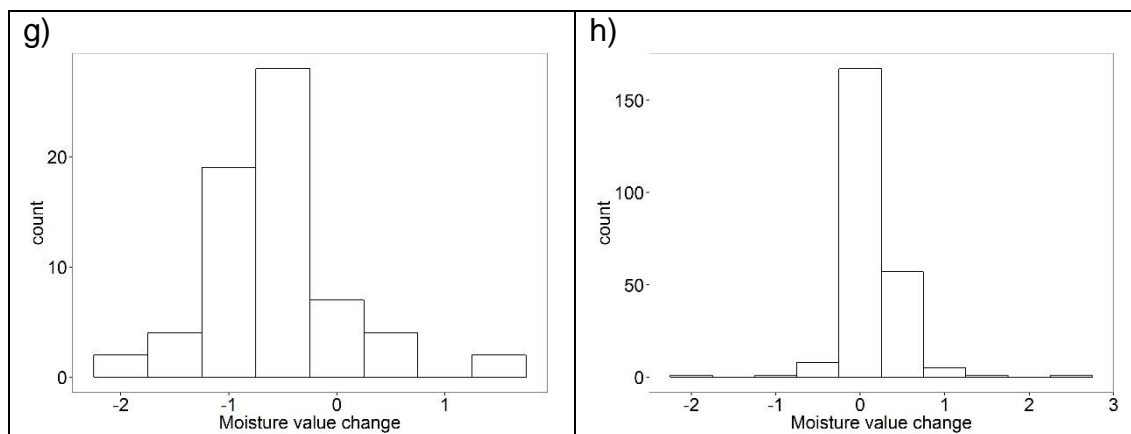


Figure S2.2. Distribution plots of the changes in mean values between periods one and two, and two and three for January temperature indicator values (a-b), July temperature indicator values (c-d), nitrogen indicator values (e-f) and moisture indicator values (g-h).

Chapter 3

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Publisher Tax ID	EU826007151
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Chapter 4

Appendix S1

Details of systematic literature review

To identify potential management techniques, we searched Web of Science for studies associated with climate change and management, covering the entire period 1900-2014. The following broad search terms associated with climate change and management types were used: (i) *climat* chang** and *manag**, (ii) *habitat stabl** and *climat* chang**, (iii) *graz** and *climat* chang**, (iv) *invasive removal* and *climat* chang** and (iv) *manag* realignment*. Querying the topic of each paper using these search terms returned a total of 50,875 paper titles, some of which were duplicates. Screening of article titles reduced this number to 721, and subsequent screening of article abstracts left a total of 101 papers that were potentially relevant. Each of these 101 papers was reviewed in detail and the reference list queried to identify further potentially relevant papers and any additional studies known to the authors were also included. A total of 62 relevant papers, upon which our review is based, was identified in this way.

Assessing the strength of evidence

The strength of evidence for each management technique was assigned a quantitative score using three criteria: (1) the magnitude of the responses reported by each study, (2) the overall confidence in the reported responses, and (3) the number of studies reporting that management technique. For each study, we first assigned scores for magnitude of responses as follows: a score of 'high' was assigned where the mean effect of management across studied organisms or locations resulted in a measured improvement of greater than 25% in the desired biological outcome (e.g. species richness or abundance); a

score of 'medium' was assigned when the mean improvement was 10-25% and a score of 'low' was assigned when the mean improvement was >0-10%.

Management techniques in which adverse responses were generally reported (i.e. the overall score was negative) are not included in Table 1.

Our assignment of scores for confidence in results are based on the authors of that study's own judgement, supplemented by analyses of confidence intervals in instances where these were reported or could be derived from e.g. measurements of standard error. 'High' confidence was assigned when 95% confidence intervals did not overlap with zero and/or when the authors' ascribed high confidence when discussing their results. 'Medium' confidence was assigned when 80% confidence intervals did not overlap with zero and/or when the authors' highlighted a few caveats when discussing their results. 'Low' confidence was assigned when 50% confidence intervals overlapped with zero or where the authors' present plausible alternative explanations for their results. In instances where analyses of confidence intervals and the authors' discussion yielded conflicting scores, the lower score was used. For each study, the scores for the magnitude and confidence were cross-tabulated (see Table S1) to derive an overall score for each study.

We do not attempt to formally quantify the confidence associated with data from multiple studies using meta-regression techniques, as the effect being measured in each study often differs and it is thus erroneous to assign higher weighting to studies with larger sample sizes. However, based on the simple premise that multiple lines of evidence for a positive effect of a management technique,

provides stronger evidence that a particular management technique will be effective when applied to un-studied organisms, where more than one study investigates the effects of a management technique, we calculated a median score across studies and cross-tabulated this against the overall number of studies to derive an overall score of the strength of evidence associated with each management technique (Table S2).

Assessing the risk of failure

The risk of failure associated with management technique was assigned a quantitative score using: (1) the likelihood of an adverse response or the intervention being ineffective (assessed using the confidence intervals surrounding each study's assessment of the impact of a management activity on flora or fauna); and (2) evidence in the wider literature not pertaining to climate change, that such management can have adverse effects. As the financial risks of an action is influenced strongly factors such as location, available budgets and the particular features of landscape or site, and site managers will be in the best position to assess this on a case-by-case basis, economic feasibility was not considered.

Our assignment of scores for risk of failure associated with each study was again based on the study author's/authors' own judgement, supplemented by analyses of confidence intervals in instances where these were reported or could be derived from e.g. measurements of standard error. High risk of failure was assigned when 50% confidence intervals overlapped with zero and/or when the authors' indicate a high likelihood of failure when discussing their results. Medium

risk of failure was assigned when measured 80% confidence intervals overlapped with zero and/or when the authors' highlighted some risk of failure when discussing their results. Low risk of failure was assigned when 80% confidence intervals did not overlap with zero or when the authors do not indicate any reason for failure.

However, in some instances, there was deemed to be a high risk of failure, even when individual studies associated with climate change and management do not allude to this, because the wider literature not pertaining to climate change either indicates directly that: a) such management can have adverse effects, or b) that the converse of a particular technique can have a beneficial effect. For example, reduced grazing generally has a high risk of failure because increased grazing has been shown to have benefits to biodiversity in some ecosystems. Our assignment of scores for a general risk of failure were derived as follows: a 'high' risk of failure was assigned when either there was (i) evidence from a wide range of study systems, or from the specific study system concerned, that the management technique in question has undesirable effects; or (ii) evidence from a wide range (> 5) of study systems, or from the specific study system concerned, that the converse or cessation of the management technique in question has beneficial effects. A 'medium' risk of failure was assigned when either there was: (i) evidence from 2 to 5 five study systems, but not the study system concerned, that the management technique in question has undesirable effects; or (ii) evidence from 2 to 5 study systems, but not the specific study system concerned, that the converse or cessation of the management technique in question has beneficial effects. In all other instances a score of 'low' was assigned. The median score derived from individual studies, and the general score derived from

wider literature, were both calculated for each management technique and that which was higher used as our final score. A summary of the criteria used to assess the risk of failure is provided below:

High:

- i. 50% Confidence intervals overlap with zero; or
- ii. Authors indicate high risk of failure when discussing their results; or
- iii. Evidence from study system in wider literature that management technique has undesirable effect; or
- iv. Evidence from >5 other study systems that management technique has undesirable effect; or
- v. Evidence from study system in wider literature that converse of management technique has desirable effect; or
- vi. Evidence from >5 other study systems that converse of management technique has desirable effect.

Medium:

If criteria for high are not met; and

- i. 80% Confidence intervals overlap with zero; or
- ii. Authors indicate some risk of failure when discussing their results; or
- iii. Evidence from 2-5 other study systems that management technique has undesirable effect; or
- iv. Evidence from 2-5 other study systems that converse of management technique has beneficial effect

If criteria for neither High nor Medium are met, then the risk is low

Appendix S2

Additional information and references associated with Table 1

Temperature Increase

Afforestation

1. Several woodland butterfly species shift to cooler, closed habitats in hot years (Suggitt *et al.* 2012) similar to those achieved by afforestation. However closed canopies may alter light availability leading to change in floral composition.
2. Tropical microhabitats provided by afforestation buffer mammals, frogs and lizards against temperature extremes (Ellis *et al.* 2010; Scheffers *et al.* 2014a; b; Hardwick *et al.* 2015). However, difficult to recreate suitable microhabitat through active management.
3. There is evidence from a range of studies that riverine shading reduces water temperatures and the frequency with which thermal thresholds for fish are exceeded (Broadmeadow & Nisbet 2004; Moore, Spittlehouse & Story 2005; Whitley *et al.* 2006; Malcolm *et al.* 2008; Broadmeadow *et al.* 2011). Parkyn *et al.* (2003) review the effectiveness of nine schemes in New Zealand and show canopy closure is required before beneficial effects are manifested, hence time-scales required can be long. McCormick & Harrison (2011) found that dense riparian tree canopy can have a negative effect on salmonid population via trophic interactions, making this a moderately risky technique.

Abandonment

4. Evidence from several studies on butterflies show they demonstrate preference for longer sward and/or reduced bare ground cover in warmer years or regions (Thomas *et al.* 1998; Davies *et al.* 2006; Suggitt *et al.* 2012) resulting from abandonment. There is a risk that longer sward may reduce light availability and increase nutrient competition for host plants. Late-successional habitats unlikely to be in short supply.

Slope creation/protection

5. Provision of equatorward facing slopes facilitates range-expanding Silver-spotted skipper butterfly through increased availability of warmer microclimates (Lawson *et al.* 2012; Bennie *et al.* 2013). The drawback is the potential reduction in availability of cool microclimate for species already present.
6. Poleward facing slopes may benefit range-retracting rainforest species and Alpine grasses as there is less long-term warming on slopes exposed to cool southerly winds in Australia (Ashcroft, Chisholm & French 2009). Effects on microclimate of slope aspect well understood (e.g. Bennie *et al.* 2008). There is a small risk of limiting availability of warm microclimates for colonising species.
7. Persistence of butterfly and high plant species threatened by climate change is generally higher in areas with high topographic heterogeneity (Suggitt *et al.* 2014, 2015). However, applied blindly this management may reduce the area of optimal microclimate. Chalk grassland swards on steeply facing sloping are more resistant to invasion by competitive grass species than those on flatter sites due to phosphorus limitation (Bennie *et al.* 2006).

Debris addition

8. Woody debris addition stabilises soil temperature and reduces moisture loss during lakeshore restoration projects, increasing overall survival of plants (Haskell *et al.* 2012). May limit light availability to smaller plants if over-applied. Two studies, from the USA (Owens *et al.* 2008) and Indonesia (Wanger *et al.* 2009) found that adding coarse woody debris to forest floors had no effect amphibian species richness or overall abundance. Two studies (Patrick, Hunter & Calhoun 2006; Semlitsch *et al.* 2009) show that most amphibian species exhibit no significant difference in abundance in clear-cuts with woody debris removed or retained.

Rainfall change

Altering grazing regimes. Livestock exclusion

9. Cattle exclusion counteracts hydrological effects of increased winter precipitation (Pyke & Marty 2005). This limits the inundation period increase resulting from precipitation increase in Californian temporary pools. Exclusion benefits invertebrates and amphibians in these pools, as they may fail to develop to maturity with extended inundation periods. Reduced grazing may result in vegetation succession and increased chance of negative effects on species from wild fires (Moreira & Russo 2007). However, high risk of failure as enhanced grazing is beneficial to ephemeral wetland species in other locations (Scott *et al.* 2012).
10. Models suggest increased grazing could counteract effects of decreased temporary pool habitat water availability in Cornwall through summer

(Maclean *et al.* 2012; Scott *et al.* 2012). Very high levels of disturbance may have undesirable consequences, though unstudied.

Creation of permeable barriers

11. The creation of permeable barriers, diversion ponds and artificial wetlands in small river catchments have well established effects on water flow (Richter *et al.* 2003; Wilkinson, Quinn & Welton 2010; Nicholson *et al.* 2012). However, the benefits to biodiversity are unexplored. No obvious risks if applied carefully.

Drainage control

12. Blocking drainage ditches increases water availability in wetlands, leading to higher crane fly abundance in dry years (Carroll *et al.* 2011), though no significant changes in wet years. No adverse effects have been reported or are likely.
13. Creating artificial drains to divert water can provide better management of wet features. This allows control of invertebrate abundance location, improving lapwing chick body condition through increased food provision (Eglington *et al.* 2008, 2010). Wet features are already present in the landscape and predation rates are unaffected through this technique (Eglington *et al.* 2009)

Irrigation/Spraying

14. Irrigation/spraying increases in-situ water availability. This has been shown to increase mating and spawning in *Pseudophryne bibronii* Günther (brown toadlet) in remnant eucalyptus forest, South-east Australia (Mitchell 2001; Shoo *et al.* 2011). Economically it is only feasible in a few

areas, which limits its applicability. Krajick (2006) shows that the installation of a sprinkler system to mitigate against reduced river flow was insufficient to prevent the Kihansi spray toad (*Nectophrynoides asperginis*) from declining rapidly in Tanzania.

Sea-level rise

Sea-defence maintenance / creation

15. Hard defences can attenuate wave strength, as well as fragmenting coastal habitats leading to increases in local biodiversity (Airolidi et al. 2005). They may also improve connectivity between rocky coast regions. Financial costs may result in only economically important areas being maintained (Richards et al. 2008) and hard defences may reduce environmental heterogeneity, leading to less diverse intertidal communities (Firth et al. 2013).
16. Creation of artificial rockpools and increasing surface texture on sea defences leads to an increased diversity of algae and sessile and mobile invertebrates (Chapman & Blockley 2009; Firth *et al.* 2013, 2014). There is no obvious risk associated with this management as it is unlikely to negatively impact rocky shore organisms though benefits may be influenced by substrate type (Green, Chapman & Blockley 2012).
17. Options for creating ecologically-engineered offshore reefs, reducing wave energy. Oysters quickly colonise cultch material (shucked oyster shells) in high and low energy environments (Piazza, Banks & La Peyre 2005). Borsje *et al.* (2011) warn that it is important to understand habitat requirements for species settlement before applying this method to ensure it isn't wasted effort.

18. Oyster and reef beds reduce wave energy (Borsje *et al.* 2011) and reduce shoreline erosion (Meyer, Townsend & Thayer 1997; Piazza, Banks & La Peyre 2005). This change is most beneficial in wave-exposed areas but these are most difficult conditions to establish reefs (Piazza, Banks & La Peyre 2005)
19. Groynes and other barriers provide stabilisation and/or accretion of material on sandy beaches and dunes. This is a widely-used management practice (Hanley *et al.* 2014) with high success rate, though may result in greater erosion elsewhere through loss of typical sediment.

Stabilisation of coastal habitat

20. Pumping of material from sediment sinks or dredging onto intertidal habitats increases the surface elevation in relation to sea level on salt marshes and sandy beaches. This leads to increased salt marsh plant biomass documented (Mendelssohn & Kuhn 2003) with the caveat that potential mineral deposition is an additional cause in this increase, as opposed to solely being the result of elevation increase. Also, the source of sediment is important, since removal from the system can increase erosion elsewhere. Fine-grained material is more likely to be washed away (Hanley *et al.* 2014).
21. Planting of ecosystem-engineering species to stabilise sediment is another widely used method for stabilisation and/or accretion of habitat. Marram grass is widely planted to stabilise dune systems, even where the species is not native (Webb, Oliver & Pik 2000). Common cordgrass was widely planted in Europe for its ability to accrete sediment (Nehring & Hesse 2008). There can be high risk associated with this method where

the species is not native, Common cordgrass is considered one of the top invasive species globally (Lowe *et al.* 2000).

Defence realignment

22. Saline inundation results in mudflat creation, providing suitable foraging habitat for wintering waterbirds (Atkinson *et al.* 2004; Badley & Allcorn 2006). Where tested, wintering waterbird community is similar to natural environments. However, where sedimentation rates are high, a shift from mudflat to salt marsh reduces suitability for feeding waders (Mazik *et al.* 2010; Morris 2013).

23. There is a rapid colonisation of new intertidal areas by a range of benthic invertebrate species (Mazik *et al.* 2010) though this is unlikely to provide a long-term fix. There are differences in abundance, diversity and community structure between a number of created and natural intertidal habitats (Craft *et al.* 1999; Mazik *et al.* 2010).

24. Newly created salt marsh allows for rapid establishment of some plant species (Mossman *et al.* 2012). Yet at some sites <50% of target species had established after 5 years (Wolters *et al.* 2008). Also characteristic perennials are rare in older, accidentally realigned sites (Mossman, Davy & Grant 2012). This may in part be because it is difficult to replicate the geomorphological and topographic heterogeneity of natural salt marshes (Verbeek & Storm 2001; Doherty & Zedler 2015).

Management of newly created intertidal habitat

25. Planting rarer species on salt marshes increases the diversity of plant communities. Recruitment of individuals following planting can be high (Zedler, Callaway & Sullivan 2001) but is dependent on the species

planted. Specifically survival is low if environmental conditions are not suitable for the species in question (Garbutt *et al.* 2006).

26. Increasing topographic heterogeneity by creating raised and lowered areas on a salt marsh increases the range of available niches. Survival and recruitment of plants varies with raising and lowering treatments (Varty & Zedler 2008; Doherty & Zedler 2015). There is little risk associated with this method, though management must be carried out prior to instatement of tidal flooding due to accessibility for earth-moving equipment.

Appendix S3

Additional information and references associated with Table 2

¹Longer vegetation could potentially provide species with cooler microhabitats. Five studies (Willems, Peet & Bik 1993; Van der Woude, Pegtel & Bakker 1994; Foster & Gross 1998; Hejcman *et al.* 2007; Honsová *et al.* 2007) show that the experimental application of nitrogen, phosphorus and/or potassium, while increasing productivity, reduced the species richness of grasslands. Numerous studies demonstrate adverse effects on species richness of nutrient enrichment and demonstrate benefits to biodiversity of reduced fertilizer application.

²Retaining areas of flooded habitat may benefit species in locations predicted to become drier. A study of rice fields in southern Brazil (Machado & Maltchik 2010) found that keeping fields flooded after harvest had no effect on amphibian species richness or abundance

³Wet habitats have been lost from agricultural systems, a problem compounded in regions predicted to become drier. Re-wetting may offer an important

mechanism for offsetting this effect, facilitating a reverse in declines. A review of three studies by Diggelen (2007) shows that re-wetting soils on old arable fields is not an effective method of restoring species-rich grassland.

⁴In habitats prone to sea-level rise, inundation with water may be a significant cause of mortality. Providing nests or nesting habitat that is protected from water (e.g. by being raised) may therefore increase reproductive success. Two studies from the USA (Koenen, Utych & Leslie 1996; Rounds, Erwin & Porter 2004) found that the nesting success of terns and waders was no higher on specially raised areas of nesting substrate, compared to unraised areas.

Table S1

Scheme for cross-tabulating scores associated with the magnitude of a response and the confidence in the response, to derive overall scores of the strength of evidence associated with each study.

		Confidence in response		
		High	Medium	Low
Magnitude of response	High	Strong	Moderate	Weak
	Medium	Strong	Moderate	Weak
	Low	Moderate	Weak	Weak

Table S2

Scheme for scoring the strength of evidence for management techniques tested in multiple studies.

		Number of studies		
		1	2-3	3+
	Strong	Strong	Strong	Strong
	Moderate/Strong *	-	Strong	Strong

Median strength of evidence for each study	Moderate	Moderate	Moderate	Strong
	Weak/Moderate *	-	Moderate	Moderate
	Weak	Weak	Weak	Moderate

*In instances where scores are derived from more than one study, the median may fall between categories, for example when one study has a score of high, and another of medium.

Table S3

Management responses to climate change, with associated effects on the environment and on wildlife. For each individual study, the strength of supporting evidence and risk of failure associated with each study and based on evidence in the wider literature is also assessed. For risk of failure, the criteria met are indicated using the numbering system shown in Appendix S1. Further details and a full list of references are provided in Appendix S2.

Adverse effect		Study	Strength of evidence from study	Risk of failure (criteria met)	Risk of failure derived from wider literature
Warming	Afforestation and abandonment / reduced grazing	Ellis <i>et al.</i> (2010)	Moderate	Low	Medium (iii,iv)
		Scheffers <i>et al.</i> (2014a)	Strong	Medium (ii)	
		Scheffers <i>et al.</i> (2014b)	Strong	Low	
		Hardwick <i>et al.</i> (2015)	Moderate	Low	
		Suggitt <i>et al.</i> (2012)	Moderate	Medium (i,ii)	
		Broadmeadow & Nisbet (2004)	Strong	Low	
		Moore, Spittlehouse & Story (2005)	Moderate	Medium (ii)	
		Whitledge <i>et al.</i> (2006)	Low	Low	
		Malcolm <i>et al.</i> (2008)	Moderate	Medium (ii)	
		Broadmeadow <i>et al.</i> (2011)	Strong	Low	
		Parkyn <i>et al.</i> (2003)	Low	Medium (ii)	
		McCormick & Harrison (2011)	Strong	Medium (ii)	
		Thomas <i>et al.</i> (1998)	Strong	Medium (ii)	
		Davies <i>et al.</i> (2006)	Moderate	Medium (ii)	
		Suggitt <i>et al.</i> (2012)	Moderate	Medium (ii)	
	Slope creation / protection	Lawson <i>et al.</i> (2012)	Strong	Medium (ii)	Medium (iii,iv)
		Bennie <i>et al.</i> (2013)	Strong	Medium (ii)	
		Ashcroft, Chisholm & French (2009)	Strong	Medium (ii)	
		Bennie <i>et al.</i> (2008)	Strong	Medium (ii)	
		Suggitt <i>et al.</i> (2014)	Strong	Medium (ii)	
		Suggitt <i>et al.</i> (2015)	Strong	Medium (ii)	
		Bennie <i>et al.</i> (2006)	Moderate	Medium (ii)	

Warming	Debris addition	Haskell <i>et al.</i> (2012)	Moderate	Medium (ii)	Medium (iii,iv)
		Owens <i>et al.</i> (2008)	Low	Low	
		Wanger <i>et al.</i> 2009	Low	Low	
		Patrick <i>et al.</i> 2006	Low	Low	
		Semlitsch <i>et al.</i> 2009	Low	Low	
Precipitation change	Altered grazing regimes	Pyke & Marty (2005)	Strong	Low	High (iii,iv,v,vi)
		Moreira & Russo (2007)	Moderate	Low	
		Scott <i>et al.</i> (2012)	Strong	High(i,ii)	
		Maclean <i>et al.</i> (2012)	Strong	High (ii)	
	Manipulate water flow with permeable or impermeable barriers or drainage control	Richter <i>et al.</i> (2003)	Moderate	Low	Low
		Wilkinson, Quinn & Welton (2010)	Strong	Low	
		Nicholson <i>et al.</i> (2012)	Strong	Low	
		Caroll <i>et al.</i> (2011)	Strong	Low	
		Eglington <i>et al.</i> (2008)	Moderate	Low	
		Eglington <i>et al.</i> (2010)	Moderate	Low	
		Eglington <i>et al.</i> (2009)	Moderate	Low	
	Irrigation/Spraying	Mitchell (2001)	Moderate	Medium (ii)	Medium (iii)
		Shoo (2011)	Moderate	Medium (ii)	
		Krajick (2006)	Low	Low	
Sea- level rise	Sea-defence creation / maintenance	Airoidi <i>et al.</i> (2005)	Moderate	Medium (ii)	Medium (iii,iv)
		Richards <i>et al.</i> (2008)	Moderate	Medium (ii)	
		Firth <i>et al.</i> (2013)	Strong	Medium (ii)	
		Chapman & Blockley (2009)	Strong	Medium (ii)	
		Firth <i>et al.</i> (2014)	Strong	Medium (ii)	
		Green, Chapman & Blockley (2012)	Strong	Medium (ii)	
		Piazza, Banks & La Peyre (2005)	Moderate	Medium (ii)	
		Borsje <i>et al.</i> (2011)	Strong	Medium (ii)	
		Meyer, Townsend & Thayer (1997)	Strong	Medium (ii)	
	Stabilisation of intertidal and coastal habitat	Hanley <i>et al.</i> (2014)	Strong	Medium (ii)	Medium (iii), (iv)
		Webb, Oliver & Pik (2000)	Strong	Medium (ii)	
		Nehring & Hesse (2008)	Strong	Medium (ii)	
		Mendelssohn & Kuhn (2003)	Strong	Low	
		Lowe <i>et al.</i> (2000)	Moderate	Medium(ii)	
	Defence realignment	Atkinson <i>et al.</i> (2004)	Strong	Low	Medium (iv)
		Badley & Allcorn (2006)	Moderate	Low	

Sea- level rise	Defence realignment	Mazik <i>et al.</i> (2010)	Moderate	Low	
		Morris (2013)	Moderate	Medium (ii)	
		Craft <i>et al.</i> (1999)	Moderate	Medium (ii)	
		Mossman <i>et al.</i> (2012)	Strong	Medium (ii)	
		Wolters <i>et al.</i> (2008)	Low	Low	
		Mossman, Davy & Grant (2012)	Low	Medium (ii)	
		Verbeek & Storm (2001)	Moderate	Medium (ii)	
		Doherty & Zedler (2015)	Strong	Low	
	Active management of newly created habitat, including seeding, re-profiling and sediment addition	Zedler, Callaway & Sullivan (2001)	Moderate	Low	Low
		Garbutt <i>et al.</i> (2006)	Moderate	Low	

Bibliography

- Airolidi, L., Abbiati, M., Beck, M.W., Hawkins, S.J., Jonsson, P.R., Martin, D., Moschella, P.S., Sundelöf, A., Thompson, R.C. & Åberg, P. (2005) An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coastal Engineering*, **52**, 1073–1087.
- Araújo, M.B., Alagador, D., Cabeza, M., Nogués-Bravo, D. & Thuiller, W. (2011) Climate change threatens European conservation areas. *Ecology Letters*, **14**, 484–492.
- Ashcroft, M.B., Chisholm, L.A. & French, K.O. (2009) Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology*, **15**, 656–667.
- Atkinson, P.W., Crooks, S., Drewitt, A., Grant, A., Rehfisch, M.M., Sharpe, J. & Tyas, C.J. (2004) Managed realignment in the UK - the first 5 years of colonization by birds. *Ibis*, **146**, 101–110.
- Badley, J. & Allcorn, R.I. (2006) Changes in bird use following the managed realignment at Freiston Shore RSPB Reserve, Lincolnshire, England. *Conservation Evidence*, **3**, 102–105.
- Barnagaud, J.-Y., Barbaro, L., Hampe, A., Jiguet, F. & Archaux, F. (2013) Species' thermal preferences affect forest bird communities along landscape and local scale habitat gradients. *Ecography*, **36**, 1218–1226.
- Barnett, T.P., Adam, J.C. & Lettenmaier, D.P. (2005) Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, **438**, 303–309.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature*, **471**, 51–57.

Barton, K. (2016) MuMIn: Multi-Model Inference.

Beaumont, L.J., Pitman, A., Perkins, S., Zimmermann, N.E., Yoccoz, N.G. & Thuiller, W. (2011) Impacts of climate change on the world's most exceptional ecoregions. *Proceedings of the National Academy of Sciences*, **108**, 2306–2311.

Beck, M.W., Brumbaugh, R.D., Airoidi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G. & Guo, X. (2011) Oyster Reefs at Risk and Recommendations for Conservation, Restoration, and Management. *BioScience*, **61**, 107–116.

Beck, E.H., Fetting, S., Knake, C., Hartig, K. & Bhattarai, T. (2007) Specific and unspecific responses of plants to cold and drought stress. *Journal of Biosciences*, **32**, 501–510.

Beer, N.A. & Joyce, C.B. (2013) North Atlantic coastal lagoons: conservation, management and research challenges in the twenty-first century. *Hydrobiologia*, **701**, 1–11.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

- Bennie, J., Hill, M.O., Baxter, R. & Huntley, B. (2006) Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, **94**, 355–368.
- Bennie, J., Hodgson, J.A., Lawson, C.R., Holloway, C.T.R., Roy, D.B., Brereton, T., Thomas, C.D. & Wilson, R.J. (2013) Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, **16**, 921–929.
- Bennie, J., Huntley, B., Wiltshire, A., Hill, M.O. & Baxter, R. (2008) Slope, aspect and climate: Spatially explicit and implicit models of topographic microclimate in chalk grassland. *Ecological Modelling*, **216**, 47–59.
- Bennie, J., Wilson, R.J., Maclean, I.M.D. & Suggitt, A.J. (2014) Seeing the woods for the trees - when is microclimate important in species distribution models? *Global Change Biology*, **20**, 2699–2700.
- Beringer, J., Hansen, L.P., Demand, J.A., Sartwell, J., Wallendorf, M. & Mange, R. (2002) Efficacy of Translocation to Control Urban Deer in Missouri: Costs, Efficiency, and Outcome. *Wildlife Society Bulletin*, **30**, 767–774.
- Beven, K.J. & Kirkby, M.J. (1979) A physically based, variable contributing area model of basin hydrology / Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. *Hydrological Sciences Bulletin*, **24**, 43–69.
- Billings, W.D. & Mooney, H.A. (1968) The Ecology of Arctic and Alpine Plants. *Biological Reviews*, **43**, 481–529.
- Birks, H.H. (2008) The Late-Quaternary history of arctic and alpine plants. *Plant*

Ecology & Diversity, **1**, 135–146.

Bluesky International Ltd. (2014) Bluesky Digital Elevation Model.

Bois, B., Pieri, P., Van Leeuwen, C., Wald, L., Huard, F., Gaudillere, J.-P. & Saur, E. (2008) Using remotely sensed solar radiation data for reference evapotranspiration estimation at a daily time step. *Agricultural and Forest Meteorology*, **148**, 619–630.

Bolam, S.G. & Whomersley, P. (2005) Development of macrofaunal communities on dredged material used for mudflat enhancement: a comparison of three beneficial use schemes after one year. *Marine Pollution Bulletin*, **50**, 40–47.

Borsje, B.W., van Wesenbeeck, B.K., Dekker, F., Paalvast, P., Bouma, T.J., van Katwijk, M.M. & de Vries, M.B. (2011) How ecological engineering can serve in coastal protection. *Ecological Engineering*, **37**, 113–122.

Bos, D., Bakker, J.P., de Vries, Y. & van Lieshout, S. (2002) Long-term vegetation changes in experimentally grazed and ungrazed back-barrier marshes in the Wadden Sea. *Applied Vegetation Science*, **5**, 45–54.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B. & Meyer, C.W. (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144–15148.

Broadmeadow, S.B., Jones, J.G., Langford, T.E.L., Shaw, P.J. & Nisbet, T.R. (2011) The influence of riparian shade on lowland stream water temperatures in southern England and their viability for brown trout. *River*

- Broadmeadow, S. & Nisbet, T.R. (2004) The effects of riparian forest management on the freshwater environment: a literature review of best management practice. *Hydrology and Earth System Sciences*, **8**, 286–305.
- Buckland, S.M., Grime, J.P., Hodgson, J.G. & Thompson, K. (1997) A Comparison of Plant Responses to the Extreme Drought of 1995 in Northern England. *Journal of Ecology*, **85**, 875–882.
- Byfield, A. (1992) Classic British wildlife sites: the Lizard Peninsula. *British Wildlife*, **3**, 92–105.
- Carroll, M.J., Dennis, P., Pearce-Higgins, J.W. & Thomas, C.D. (2011) Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology*, **17**, 2991–3001.
- Chapman, M.G. & Blockley, D.J. (2009) Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. *Oecologia*, **161**, 625–635.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, **333**, 1024–1026.
- Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and Competition on Gradients in Alpine Plant Communities. *Ecology*, **82**, 3295–3308.
- Clausen, K.K., Stjernholm, M. & Clausen, P. (2013) Grazing management can counteract the impacts of climate change-induced sea level rise on salt marsh-dependent waterbirds. *Journal of Applied Ecology*, **50**, 528–537.

- Clavero, M., Benejam, L. & Seglar, A. (2009) Microhabitat use by foraging white-clawed crayfish (*Austropotamobius pallipes*) in stream pools in the NE Iberian Peninsula. *Ecological Research*, **24**, 771–779.
- Coombe, D.E. & Frost, L.C. (1956) The Heaths of the Cornish Serpentine. *Journal of Ecology*, **44**, 226–256.
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K. & Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology and Evolution*, **11**, 362–366.
- Craft, C., Reader, J., Sacco, J.N. & Broome, S.W. (1999) Twenty-five years of ecosystem development of constructed *Spartina alterniflora* (Loisel) marshes. *Ecological Applications*, **9**, 1405–1419.
- Crooks, S., Schutten, J., Sheern, G.D., Pye, K. & Davy, A.J. (2002) Drainage and Elevation as Factors in the Restoration of Salt Marsh in Britain. *Restoration Ecology*, **10**, 591–602.
- Curtis, R.J. & Isaac, N.J.B. (2015) The effect of temperature and habitat quality on abundance of the Glanville fritillary on the Isle of Wight: implications for conservation management in a warming climate. *Journal of Insect Conservation*, **19**, 217–225.
- Danahar, D. (2011) *The Dorothy Stringer High School Butterfly Haven. The Sussex Butterfly Report 2011*. Brighton.
- Davies, Z.G., Wilson, R.J., Coles, S. & Thomas, C.D. (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. *Journal of Animal Ecology*, **75**,

247–256.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C. & Mace, G.M. (2011) Beyond Predictions: Biodiversity Conservation in a Changing Climate. *Science*, **332**, 53–58.

Defra. (2013) *Biodiversity Offsetting in England. Green Paper*. London.

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, **16**, 646–655.

Diggelen, R. Van. (2007) Habitat creation: nature conservation of the future? *Aspects of Applied Biology*, **82**, 1–11.

Doherty, J.M. & Zedler, J.B. (2015) Increasing substrate heterogeneity as a bet-hedging strategy for restoring wetland vegetation. *Restoration Ecology*, **23**, 15–25.

Early, R. & Sax, D.F. (2014) Climatic niche shifts between species ' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. , 1356–1365.

Eglington, S.M., Bolton, M., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Gill, J.A. (2010) Managing water levels on wet grasslands to improve foraging conditions for breeding northern lapwing *Vanellus vanellus*. *Journal of Applied Ecology*, **47**, 451–458.

Eglington, S.M., Gill, J.A., Bolton, M., Smart, M.A., Sutherland, W.J. & Watkinson, A.R. (2008) Restoration of wet features for breeding waders on lowland grassland. *Journal of Applied Ecology*, **45**, 305–314.

- Eglington, S.M., Gill, J.A., Smart, M.A., Sutherland, W.J., Watkinson, A.R. & Bolton, M. (2009) Habitat management and patterns of predation of Northern Lapwings on wet grasslands: The influence of linear habitat structures at different spatial scales. *Biological Conservation*, **142**, 314–324.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (1991) *Zeigerwerte von Pflanzen in Mitteleuropa*. Göttingen.
- Ellis, W., Melzer, A., Clifton, I.D. & Carrick, F. (2010) Climate change and the koala *Phascolarctos cinereus*: water and energy. *Australian Zoologist*, **35**, 369–377.
- ESRI. (2014) ArcGIS Desktop: Release 10.2.
- Firth, L.B., Mieszkowska, N., Thompson, R.C. & Hawkins, S.J. (2013) Climate change and adaptational impacts in coastal systems: the case of sea defences. *Environmental Science: Processes & impacts*, **15**, 1665–1670.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoidi, L., Bouma, T.J., Bozzeda, F., Ceccherelli, V.U., Colangelo, M.A., Evans, A., Ferrario, F., Hanley, M.E., Hinz, H., Hoggart, S.P.G., Jackson, J.E., Moore, P., Morgan, E.H., Perkol-Finkel, S., Skov, M.W., Strain, E.M., van Belzen, J. & Hawkins, S.J. (2014) Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, **87**, 122–135.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global Consequences of Land Use.

- Science*, **309**, 570–574.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. & Holling, C.S. (2004) Regime Shifts, Resilience, and Biodiversity in Ecosystem Management. *Annual Review of Ecology, Evolution, and Systematics*, **35**, 557–581.
- Forister, M.L., McCall, A.C., Sanders, N.J., Fordyce, J.A., Thorne, J.H., O'Brien, J., Waetjen, D.P. & Shapiro, A.M. (2010) Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 2088–2092.
- Foster, B.L. & Gross, K.L. (1998) Species Richness in a Successional Grassland : Effects of Nitrogen Enrichment and Plant Litter. *Ecology*, **79**, 2593–2602.
- Franklin, J., Davis, F.W., Ikegami, M., Syphard, A.D., Flint, L.E., Flint, A.L. & Hannah, L. (2013) Modeling plant species distributions under future climates: how fine scale do climate projections need to be? *Global Change Biology*, **19**, 473–483.
- French, P.W. (2001) *Coastal Defences: Processes, Problems and Solutions*. Routledge, London, UK.
- French, P.W. (2006) Managed realignment – The developing story of a comparatively new approach to soft engineering. *Estuarine, Coastal and Shelf Science*, **67**, 409–423.
- French, C.N. (2010) Recording in Cornwall 2006 to 2009. *Botanical Cornwall*, **14**, 9–14.

De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, J., Decocq, G.M., Dierschke, H., Eriksson, O., Gilliam, F.S., Hédli, R., Heinken, T., Hermy, M., Hommel, P., Jenkins, M.A., Kelly, D.L., Kirby, K.J., Mitchell, F.J., Naaf, T., Newman, M., Peterken, G., Petřík, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J. & Verheyen, K. (2013) Microclimate moderates plant responses to macroclimate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 18561–18565.

Garbutt, R.A., Reading, C.J., Wolters, M., Gray, A.J. & Rothery, P. (2006) Monitoring the development of intertidal habitats on former agricultural land after the managed realignment of coastal defences at Tollesbury, Essex, UK. *Marine Pollution Bulletin*, **53**, 155–164.

Geiger, R. (1965) *The Climate Near the Ground*. Harvard University Press, Cambridge, MA.

Gillingham, P.K., Bradbury, R.B., Roy, D.B., Anderson, B.J., Baxter, J.M., Bourn, N.A.D., Crick, H.Q.P., Findon, R.A., Fox, R., Franco, A., Hill, J.K., Hodgson, J.A., Holt, A.R., Morecroft, M.D., O'Hanlon, N.J., Oliver, T.H., Pearce-Higgins, J.W., Procter, D.A., Thomas, J.A., Walker, K.J., Walmsley, C.A., Wilson, R.J. & Thomas, C.D. (2015) The effectiveness of protected areas in the conservation of species with changing geographical ranges. *Biological Journal of the Linnean Society*, **115**, 707–717.

Gillingham, P.K., Huntley, B., Kunin, W.E. & Thomas, C.D. (2012) The effect of

- spatial resolution on projected responses to climate warming. *Diversity and Distributions*, **18**, 990–1000.
- Gleason, M., McCreary, S., Miller-Henson, M., Ugoretz, J., Fox, E., Merrifield, M., McClintock, W., Serpa, P. & Hoffman, K. (2010) Science-based and stakeholder-driven marine protected area network planning: A successful case study from north central California. *Ocean and Coastal Management*, **53**, 52–68.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J.L.B., Coldea, G., Dick, J., Erschbamer, B., Calzado, M.R.F., Kazakis, G., Krajči, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Puscas, M., Rossi, G., Stanisci, A., Theurillat, J.-P., Tomaselli, M., Villar, L., Vittoz, P., Vogiatzakis, I. & Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, **2**, 111–115.
- Green, D.S., Chapman, M.G. & Blockley, D.J. (2012) Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecological Engineering*, **46**, 1–10.
- Greenwood, O., Mossman, H.L., Suggitt, A.J., Curtis, R.J. & Maclean, I.M.D. (2016) Using in situ management to conserve biodiversity under climate change. *Journal of Applied Ecology*, **53**, 885–894.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology: A Functional Approach to Common British Species*. Unwin Hyman, London.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, **8**, 993–1009.

- Guy, C. (2003) Freezing tolerance of plants: current understanding and selected emerging concepts. *Canadian Journal of Botany*, **81**, 1216–1223.
- Hanley, M.E., Hoggart, S.P.G., Simmonds, D.J., Bichot, A., Colangelo, M.A., Bozzeda, F., Heurtefeux, H., Ondiviela, B., Ostrowski, R., Recio, M., Trude, R., Zawadzka-Kahlau, E. & Thompson, R.C. (2014) Shifting sands? Coastal protection by sand banks, beaches and dunes. *Coastal Engineering*, **87**, 136–146.
- Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B. & McCullough, I.M. (2014) Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. *Trends in Ecology and Evolution*, **29**, 390–397.
- Hapke, C.J., Kratzmann, M.G. & Himmelstoss, E.A. (2013) Geomorphic and human influence on large-scale coastal change. *Geomorphology*, **199**, 160–170.
- Hardwick, S.R., Toumi, R., Pfeifer, M., Turner, E.C., Nilus, R. & Ewers, R.M. (2015) The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: Forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, **201**, 187–195.
- Haskell, D.E., Flaspohler, D.J., Webster, C.R. & Meyer, M.W. (2012) Variation in Soil Temperature, Moisture, and Plant Growth with the Addition of Downed Woody Material on Lakeshore Restoration Sites. *Restoration Ecology*, **20**, 113–121.
- Haugen, R.K. & Brown, J. (1980) Coastal-Inland Distributions of Summer Air Temperature and Precipitation in Northern Alaska. *Arctic and Alpine*

Research, **12**, 403–412.

Havens, K.E. (2008) Cyanobacteria blooms: effects on aquatic ecosystems.

Cyanobacterial Harmful Algal Blooms: State of the Science and Research Needs, pp. 733–747. Springer, New York.

Hay, C.C., Morrow, E., Kopp, R.E. & Mitrovica, J.X. (2015) Probabilistic reanalysis of twentieth-century sea-level rise. *Nature*, **517**, 481–484.

Hejcman, M., Klauisová, M., Schellberg, J. & Honsová, D. (2007) The Rengen Grassland Experiment: Plant species composition after 64 years of fertilizer application. *Agriculture, Ecosystems and Environment*, **122**, 259–266.

Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hill, M.O., Preston, C.D. & Roy, D.B. (2004) *Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats*. Penicuik.

Hobson, P. & Mickleburgh, P. (2008) Ancient woodlands and climate change: Old growth structures matter. *Quarterly Journal of Forestry*, **103**, 95.

Hofierka, J. & Šúri, M. (2002) The solar radiation model for Open source GIS: implementation and applications. *Proceedings of the Open source GIS-GRASS users conference*, 11–13.

Honsová, D., Hejcman, M., Klauisová, M., Pavlů, V., Kocourková, D. & Hakl, J. (2007) Species composition of an alluvial meadow after 40 years of applying nitrogen, phosphorus and potassium fertilizer. *Preslia*, **79**, 245–258.

- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, **486**, 105–108.
- Hopkins, J.J., Allison, H.M., Walmsley, C.A., Gaywood, M. & Thurgate, G. (2007) *Conserving Biodiversity in a Changing Climate: Guidance on Building Capacity to Adapt*. London.
- Howarth, R.W. (2008) Coastal nitrogen pollution: A review of sources and trends globally and regionally. *Harmful Algae*, **8**, 14–20.
- Ingestad, T. (1977) Nitrogen and plant growth; maximum efficiency of nitrogen fertilizers. *Ambio*, **6**, 146–151.
- IPCC. (2013) *Climate Change 2013: The Physical Science Basis*. Cambridge.
- IUCN. (2017) The IUCN Redlist of Threatened Species, <http://www.iucnredlist.org>
- Jackson, A.C. & McIlvenny, J. (2011) Coastal squeeze on rocky shores in northern Scotland and some possible ecological impacts. *Journal of Experimental Marine Biology and Ecology*, **400**, 314–321.
- Johns, C.A. (1848) *A Week at The Lizard*, 1st ed. Society for Promoting Christian Knowledge, London, UK.
- Jump, A.S. & Peñuelas, J. (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.
- Kearney, N., Handasyde, K., Ward, S. & Kearney, M. (2007) Fine-scale

- microhabitat selection for dense vegetation in a heathland rodent, *Rattus lutreolus*: Insights from intraspecific and temporal patterns. *Austral Ecology*, **32**, 315–325.
- Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, **12**, 334–350.
- Koenen, M.T., Utych, R.B. & Leslie, D.M. (1996) Methods Used to Improve Least Tern and Snowy Plover Nesting Success on Alkaline Flats. *Journal of Field Ornithology*, **67**, 281–291.
- Körner, C. (2002) Alpine plants: stressed or adapted? *Physiological Plant Ecology: 39th Symposium of the British Ecological Society* (eds M.C. Press, J.D. Scholes, & M.G. Barker), pp. 297–312. Cambridge University Press, Cambridge.
- Kosanic, A., Anderson, K., Frère, C.H. & Harrison, S. (2015) Regional vegetation change and implications for local conservation: An example from West Cornwall (United Kingdom). *Global Ecology and Conservation*, **4**, 405–413.
- Kosanic, A., Anderson, K., Harrison, S., Turkington, T. & Bennie, J. (2018) Changes in the geographical distribution of plant species and climatic variables on the West Cornwall peninsula (South West UK). *Plos One*, **13**, e0191021.
- Krajick, K. (2006) The Lost World of the Kihansi Toad. *Science*, **311**, 1230–1232.
- Krauss, K.W., McKee, K.L., Lovelock, C.E., Cahoon, D.R., Saintilan, N., Reef, R. & Chen, L. (2014) How mangrove forests adjust to rising sea level. *New*

Phytologist, **202**, 19–34.

Kudo, G., Kawai, Y., Amagai, Y. & Winkler, D.E. (2017) Degradation and recovery of an alpine plant community: experimental removal of an encroaching dwarf bamboo. *Alpine Botany*, **127**, 75–83.

Lawlor, D.W., Lemaire, G. & Gastal, F. (2001) Nitrogen, Plant Growth and Crop Yield. *Plant Nitrogen*, pp. 343–367. Springer, Berlin.

Lawson, C.R., Bennie, J.J., Thomas, C.D., Hodgson, J.A. & Wilson, R.J. (2012) Local and landscape management of an expanding range margin under climate change. *Journal of Applied Ecology*, **49**, 552–561.

Lawson, C.R., Vindenes, Y., Bailey, L. & van de Pol, M. (2015) Environmental variation and population responses to global change. *Ecology Letters*, **18**, 724–736.

Lenane, R. (2012) *Keeping Rivers Cool: Getting Ready for Climate Change by Creating Riparian Shade*. Bristol.

Liancourt, P., Callaway, R.M. & Michalet, R. (2005) Stress Tolerance and Competitive-Response Ability Determine the Outcome of Biotic Interactions. *Ecology*, **86**, 1611–1618.

Lin, B.B. (2007) Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. *Agricultural and Forest Meteorology*, **144**, 85–94.

Liu, J., Linerman, M., Ouyang, Z., An, L., Yang, J. & Zhang, H. (2001) Ecological Degradation in Protected Areas: The Case of Wolong Nature Reserve for Giant Pandas. *Science*, **292**, 98–101.

- Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) *100 of the World's Worst Invasive Alien Species: A Selection from the Global Invasive Species Database*. The Invasive Species Specialist Group, Auckland.
- Lunt, I.D., Jansen, A. & Binns, D.L. (2012) Effects of flood timing and livestock grazing on exotic annual plants in riverine floodplains. *Journal of Applied Ecology*, **49**, 1131–1139.
- Luoto, M. & Heikkinen, R.K. (2008) Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology*, **14**, 483–494.
- Luoto, M., Pykälä, J. & Kuussaari, M. (2003) Decline of landscape-scale habitat and species diversity after the end of cattle grazing. *Journal for Nature Conservation*, **11**, 171–178.
- Macgregor, N.A. & van Dijk, N. (2014) Adaptation in Practice: How Managers of Nature Conservation Areas in Eastern England are Responding to Climate Change. *Environmental Management*, **54**, 700–719.
- Machado, I.F. & Maltchik, L. (2010) Can management practices in rice fields contribute to amphibian conservation in southern Brazilian wetlands? *Aquatic Conservation: Marine and Freshwater Ecosystems*, **20**, 39–46.
- Maclean, I.M.D., Bennie, J.J., Scott, A.J. & Wilson, R.J. (2012) A high-resolution model of soil and surface water conditions. *Ecological Modelling*, **237–238**, 109–119.
- Maclean, I.M.D., Hopkins, J.J., Bennie, J., Lawson, C.R. & Wilson, R.J. (2015) Microclimates buffer the responses of plant communities to climate change.

- Global Ecology and Biogeography*, **24**, 1340–1350.
- Macleán, I.M.D., Suggitt, A.J., Wilson, R.J., Duffy, J.P. & Bennie, J.J. (2017) Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology*, **23**, 256–268.
- Macleán, I.M.D. & Wilson, R.J. (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 12337–12342.
- Malcolm, I.A., Soulsby, C., Hannah, D.M., Bacon, P.J., Youngson, A.F. & Tetzlaff, D. (2008) The influence of riparian woodland on stream temperatures: implications for the performance of juvenile salmonids. *Hydrological Processes*, **22**, 968–979.
- Malloch, A.J.C. (1971) Vegetation of the maritime cliff-tops of the Lizard and Land's End peninsulas, west Cornwall. *New Phytologist*, **70**, 1155–1197.
- Mantyka-Pringle, C.S., Martin, T.G., Moffatt, D.B., Linke, S. & Rhodes, J.R. (2014) Understanding and predicting the combined effects of climate change and land-use change on freshwater macroinvertebrates and fish. *Journal of Applied Ecology*, **51**, 572–581.
- Mantyka-Pringle, C.S., Martin, T.G. & Rhodes, J.R. (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.
- Maskell, L.C., Crowe, A., Dunbar, M.J., Emmett, B., Henrys, P., Keith, A.M., Norton, L.R., Scholefield, P., Clark, D.B., Simpson, I.C. & Smart, S.M. (2013)

- Exploring the ecological constraints to multiple ecosystem service delivery and biodiversity. *Journal of Applied Ecology*, **50**, 561–571.
- Mazik, K., Musk, W., Dawes, O., Solyanko, K., Brown, S., Mander, L. & Elliott, M. (2010) Managed realignment as compensation for the loss of intertidal mudflat: A short term solution to a long term problem? *Estuarine, Coastal and Shelf Science*, **90**, 11–20.
- McCormick, D.P. & Harrison, S.S.C. (2011) Direct and indirect effects of riparian canopy on juvenile Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*, in south-west Ireland. *Fisheries Management and Ecology*, **18**, 444–455.
- McMahon, S.M., Harrison, S.P., Armbruster, W.S., Bartlein, P.J., Beale, C.M., Edwards, M.E., Kattge, J., Midgley, G., Morin, X. & Prentice, I.C. (2011) Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. *Trends in Ecology and Evolution*, **26**, 249–259.
- McRae, B.H., Hall, S.A., Beier, P. & Theobald, D.M. (2012) Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. *PLoS ONE*, **7**.
- Mendelssohn, I.A. & Kuhn, N.L. (2003) Sediment subsidy: Effects on soil-plant responses in a rapidly submerging coastal salt marsh. *Ecological Engineering*, **21**, 115–128.
- Menéndez, R., Megías, A.G., Hill, J.K., Braschler, B., Willis, S.G., Collingham, Y., Fox, R., Roy, D.B. & Thomas, C.D. (2006) Species richness changes lag behind climate change. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 1465–1470.

- Meyer, D.L., Townsend, E.C. & Thayer, G.W. (1997) Stabilization and Erosion Control Value of Oyster Cultch for Intertidal Marsh. *Restoration Ecology*, **5**, 93–99.
- Millenium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, D.C.
- Mitchell, N.J. (2001) Males call more from wetter nests: effects of substrate water potential on reproductive behaviours of terrestrial toadlets. *Proceedings of the Royal Society of London B: Biological Sciences*, **268**, 87–93.
- Mitchell, R.J., Morecroft, M.D., Acreman, M., Crick, H.Q.P., Frost, M., Harley, M., Maclean, I.M.D., Mountford, O., Piper, J., Pontier, H., Rehfisch, M.M., Ross, L.C., Smithers, R.J., Stott, A., Walmsley, C., Watts, O. & Wilson, E. (2007) *England Biodiversity Strategy - Towards Adaptation to Climate Change*. Department for Environment, Food and Rural Affairs, London.
- Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Ejrnæs, R., Odgaard, M.V. & Svenning, J.C. (2013) Topographically controlled soil moisture drives plant diversity patterns within grasslands. *Biodiversity and Conservation*, **22**, 2151–2166.
- Molles, L.E., Calcott, A., Peters, D., Delamare, G., Hudson, J., Innes, J., Flux, I. & Wass, J. (2008) ‘Acoustic anchoring’ and the successful translocation of North Island kokako (*Callaeas cinerea wilsoni*) to a New Zealand mainland management site within continuous forest. *Notornis*, **55**, 57–68.
- Moore, R.D., Spittlehouse, D.L. & Story, A. (2005) Riparian Microclimate and Stream Temperature Response to Forest Harvesting: A Review. *Journal Of The American Water Resources Association*, **41**, 813–834.

- Morecroft, M.D., Taylor, M.E. & Oliver, H.R. (1998) Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology*, **90**, 141–156.
- Moreira, F. & Russo, D. (2007) Modelling the impact of agricultural abandonment and wildfires on vertebrate diversity in Mediterranean Europe. *Landscape Ecology*, **22**, 1461–1476.
- Morris, R.K.A. (2013) Managed realignment as a tool for compensatory habitat creation – A re-appraisal. *Ocean & Coastal Management*, **73**, 82–91.
- Morris, R.K.A., Reach, I.S., Duffy, M.J., Collins, T.S. & Leafe, R.N. (2004) On the loss of saltmarshes in south-east England and the relationship with *Nereis diversicolor*. *Journal of Applied Ecology*, **41**, 787–791.
- Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. & Simpson, I.C. (2011) Countryside Survey: Final Report for LCM2007 – the new UK Land Cover Map. , 112 (CEH Project Number: C03259).
- Mossman, H.L., Brown, M.J.H., Davy, A.J. & Grant, A. (2012) Constraints on Salt Marsh Development Following Managed Coastal Realignment: Dispersal Limitation or Environmental Tolerance? *Restoration Ecology*, **20**, 65–75.
- Mossman, H.L., Davy, A.J. & Grant, A. (2012) Does managed coastal realignment create saltmarshes with ‘equivalent biological characteristics’ to natural reference sites? *Journal of Applied Ecology*, **49**, 1446–1456.
- Moudrý, V. & Šímová, P. (2012) Influence of positional accuracy, sample size and scale on modelling species distributions: a review. *International Journal of Geographical Information Science*, **26**, 2083–2095.

Natural England (2010) *Illustrated Guide to Ponds and Scrapes*. York.

Natural England (2017) MAGIC Map,
<http://www.natureonthemap.naturalengland.org.uk/MagicMap.aspx>

Nature After Minerals (2015) *Working Together to Restore Quarries for People and Wildlife*. RSPB, Sandy.

Nehring, S. & Hesse, K.J. (2008) Invasive alien plants in marine protected areas: The *Spartina anglica* affair in the European Wadden Sea. *Biological Invasions*, **10**, 937–950.

Nicholson, A.R., Wilkinson, M.E., O'Donnell, G.M. & Quinn, P.F. (2012) Runoff attenuation features: a sustainable flood mitigation strategy in the Belford catchment, UK. *Area*, **44**, 463–469.

O'Connell, P.E., Ewen, J., O'Donnell, G. & Quinn, P. (2007) Is there a link between agricultural land-use management and flooding? *Hydrology and Earth System Sciences*, **11**, 96–107.

Oliver, T.H., Brereton, T. & Roy, D.B. (2013) Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography*, **36**, 579–586.

Oliver, T.H. & Morecroft, M.D. (2014) Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. *Wiley Interdisciplinary Reviews: Climate Change*, **5**, 317–335.

Owens, A.K., Moseley, K.R., McCay, T.S., Castleberry, S.B., Kilgo, J.C. & Ford, W.M. (2008) Amphibian and reptile community response to coarse woody debris manipulations in upland loblolly pine (*Pinus taeda*) forests. *Forest*

Ecology and Management, **256**, 2078–2083.

Parkyn, S.M., Davies-Colley, R.J., Halliday, N.J., Costley, K.J. & Croker, G.F.

(2003) Planted Riparian Buffer Zones in New Zealand: Do They Live Up to Expectations? *Restoration Ecology*, **11**, 436–447.

Patrick, D.A., Hunter, M.L. & Calhoun, A.J.K. (2006) Effects of experimental

forestry treatments on a Maine amphibian community. *Forest Ecology and Management*, **234**, 323–332.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D., Payn, T.W., Paquette, A. &

Parrotta, J.A. (2013) Plantation forests, climate change and biodiversity. *Biodiversity and Conservation*, **22**, 1203–1227.

Pearman, D.A. (2017) The population dynamics of rare annual plants on the

Lizard Peninsula, Cornwall, UK, 2009–2016. *New Journal of Botany*, **7**, 11–24.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change

on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, **12**, 361–371.

Penna, D., Borga, M., Norbiato, D. & Fontana, G.D. (2009) Hillslope scale soil

moisture variability in a steep alpine terrain. *Journal of Hydrology*, **364**, 311–327.

Phillips, S.J., Dudík, M. & Schapire, R.E. (2004) A maximum entropy approach

to species distribution modeling. *21st International Conference on Machine Learning, Banff, Canada*, 655–662.

Piazza, B.P., Banks, P.D. & La Peyre, M.K. (2005) The Potential for Created

- Oyster Shell Reefs as a Sustainable Shoreline Protection Strategy in Louisiana. *Restoration Ecology*, **13**, 499–506.
- Pigott, C.D. (1968) *Cirsium acaulon* (L.) Scop. *Journal of Ecology*, **56**, 597–612.
- Potter, K.A., Woods, H.A. & Pincebourde, S. (2013) Microclimatic challenges in global change biology. *Global Change Biology*, **19**, 2932–2939.
- Preston, C.D. & Hill, M.O. (1997) The geographical relationships of British and Irish vascular plants. *Botanical Journal of the Linnean Society*, **124**, 1–120.
- Preston, J.C. & Sandve, S.R. (2013) Adaptation to seasonality and the winter freeze. *Frontiers in Plant Science*, **4**, 1–18.
- Pyke, C.R. & Marty, J. (2005) Cattle Grazing Mediates Climate Change Impacts on Ephemeral Wetlands. *Conservation Biology*, **19**, 1619–1625.
- R Core Team (2016) R: A language and environment for statistical computing.
- Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz, P., Thuiller, W. & Guisan, A. (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, **15**, 1557–1569.
- Rannow, S., Macgregor, N.A., Albrecht, J., Crick, H.Q.P., Förster, M., Heiland, S., Janauer, G., Morecroft, M.D., Neubert, M., Sarbu, A. & Sienkiewicz, J. (2014) Managing Protected Areas Under Climate Change: Challenges and Priorities. *Environmental Management*, **54**, 732–743.
- Ratcliffe, D.A. (1977) *The Selection of Biological Sites of National Importance to Nature Conservation in Britain*. Cambridge University Press, Cambridge.

RECOVER. (2014) *System Status Report August 2014*. Jacksonville and West Palm Beach, FL.

Richards, J.A., Mokrech, M., Berry, P.M. & Nicholls, R.J. (2008) Regional assessment of climate change impacts on coastal and fluvial ecosystems and the scope for adaptation. *Climatic Change*, **90**, 141–167.

Richter, B.D., Mathews, R., Harrison, D.L. & Wigington, R. (2003) Ecologically sustainable water management: Managing river flows for ecological integrity. *Ecological Applications*, **13**, 206–224.

Rodriguez, A.B., Fodrie, F.J., Ridge, J.T., Lindquist, N.L., Theuerkauf, E.J., Coleman, S.E., Grabowski, J.H., Brodeur, M.C., Gittman, R.K., Keller, D.A. & Kenworthy, M.D. (2014) Oyster reefs can outpace sea-level rise. *Nature Climate Change*, **4**, 493–497.

Rounds, R.A., Erwin, R.M. & Porter, J.H. (2004) Nest-site selection and hatching success of waterbirds in coastal Virginia: some results of habitat manipulation. *Journal of Field Ornithology*, **75**, 317–329.

RSPB. (2013) *Tackling Climate Change-Related Threats to an Important Coastal SPA in Eastern England. Final Technical Report to LIFE+*. RSPB, Sandy.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001) Catastrophic shifts in ecosystems. *Nature*, **413**, 591–596.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E. & Evans, T.A. (2014a) Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, **20**, 495–503.

Scheffers, B.R., Evans, T.A., Williams, S.E. & Edwards, D.P. (2014b)

Microhabitats in the tropics buffer temperature in a globally coherent manner.

Biology Letters, **10**, 20140819.

Scherrer, D. & Körner, C. (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.

Scott, A., Maclean, I.M.D., Byfield, A., Pay, A.R. & Wilson, R.J. (2012) Artificial disturbance promotes recovery of rare Mediterranean Temporary Pond plant species on the Lizard Peninsula, Cornwall, England. *Conservation Evidence*, **9**, 79–86.

Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D.A., Rittenhouse, T.A.G. & Rothermel, B.B. (2009) Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments. *BioScience*, **59**, 853–862.

Seo, C., Thorne, J.H., Hannah, L. & Thuiller, W. (2009) Scale effects in species distribution models: implications for conservation planning under climate change. *Biology Letters*, **5**, 39–43.

Shi, Z., Sherry, R., Xu, X., Hararuk, O., Souza, L., Jiang, L., Xia, J., Liang, J. & Luo, Y. (2015) Evidence for long-term shift in plant community composition under decadal experimental warming. *Journal of Ecology*, **103**, 1131–1140.

Shoo, L.P., Olson, D.H., McMenamin, S.K., Murray, K.A., Van Sluys, M., Donnelly, M.A., Stratford, D., Terhivuo, J., Merino-Viteri, A., Herbert, S.M., Bishop, P.J., Corn, P.S., Dovey, L., Griffiths, R.A., Lowe, K., Mahony, M., McCallum, H., Shuker, J.D., Simpkins, C., Skerratt, L.F., Williams, S.E. &

- Hero, J.-M. (2011) Engineering a future for amphibians under climate change. *Journal of Applied Ecology*, **48**, 487–492.
- Slater, M. (2014) *Creating Scrapes for Butterflies & Moths*. Butterfly Conservation, Wareham.
- Spencer, T. & Brooks, S.M. (2012) Methodologies for measuring and modelling change in coastal saline lagoons under historic and accelerated sea-level rise, Suffolk coast, eastern England. *Hydrobiologia*, **693**, 99–115.
- Stein, E.D., Cover, M.R., Fetscher, A.E., O'Reilly, C., Guardado, R. & Solek, C.W. (2013) Reach-scale geomorphic and biological effects of localized streambank armoring. *Journal of the American Water Resources Association*, **49**, 780–792.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K. & Lima, M. (2002) Ecological Effects of Climate Fluctuations. *Ecology & Climatology*, **297**, 1292–1296.
- Stevens, C.J., Dise, N.B., Mountford, J.O. & Gowing, D.J. (2004) Impact of Nitrogen Deposition on the Species Richness of Grasslands. *Science*, **303**, 1876–1879.
- Stevens, J.T., Safford, H.D., Harrison, S. & Latimer, A.M. (2015) Forest disturbance accelerates thermophilization of understory plant communities. *Journal of Ecology*, **103**, 1253–1263.
- Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. (2011) Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos*, **120**, 1–8.

- Suggitt, A.J., Stefanescu, C., Páramo, F., Oliver, T., Anderson, B.J., Hill, J.K., Roy, D.B., Brereton, T. & Thomas, C.D. (2012) Habitat associations of species show consistent but weak responses to climate. *Biology Letters*, **8**, 590–593.
- Suggitt, A.J., Wilson, R.J., August, T.A., Beale, C.M., Bennie, J.J., Dordolo, A., Fox, R., Hopkins, J.J., Isaac, N.J.B., Jorieux, P., MacGregor, N.A., Marcetteau, J., Massimino, D., Morecroft, M.D., Pearce-Higgins, J.W., Walker, K. & Maclean, I.M.D. (2014) *Climate Change Refugia for the Flora and Fauna of England*. Natural England, London.
- Suggitt, A.J., Wilson, R.J., August, T.A., Fox, R., Isaac, N.J.B., Macgregor, N.A., Morecroft, M.D. & Maclean, I.M.D. (2015) Microclimate affects landscape level persistence in the British Lepidoptera. *Journal of Insect Conservation*, **19**, 237–253.
- Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.
- Sutherland, W.J. (2006) Predicting the ecological consequences of environmental change: a review of the methods*. *Journal of Applied Ecology*, **43**, 599–616.
- Tate, A.S. & Battaglia, L.L. (2013) Community disassembly and reassembly following experimental storm surge and wrack application. *Journal of Vegetation Science*, **24**, 46–57.
- Tesauro, J. & Ehrenfeld, D. (2007) The Effects of Livestock Grazing on the Bog Turtle [*Glyptemys* (= *clemmys*) *muhlenbergii*]. *Herpetologica*, **63**, 293–300.

- Thomas, C.D. (2011) Translocation of species, climate change, and the end of trying to recreate past ecological communities. *Trends in Ecology & Evolution*, **26**, 216–221.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thomas, C.D. & Gillingham, P.K. (2015) The performance of protected areas for biodiversity under climate change. *Biological Journal of the Linnean Society*, **115**, 718–730.
- Thomas, C.D. & Palmer, G. (2015) Non-native plants add to the British flora without negative consequences for native diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 4387–4392.
- Thomas, J.A. (1993) Holocene climate changes and warm man-made refugia may explain why a 6th of British butterflies possess unnatural early-successional habitats. *Ecography*, **16**, 278–284.
- Thomas, J.A., Simcox, D.J. & Hovestadt, T. (2011) Evidence based conservation of butterflies. *Journal of Insect Conservation*, **15**, 241–258.
- Thomas, J.A., Simcox, D.J., Wardlaw, J.C., Elmes, G.W., Hochberg, M.E. & Clarke, R.T. (1998) Effects of latitude, altitude and climate on the habitat and conservation of the endangered butterfly *Maculinea arion* and its *Myrmica* ant hosts. *Journal of Insect Conservation*, **2**, 39–46.

- Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T. & Prentice, I.C. (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.
- Trathan, P.N., García-Borboroglu, P., Boersma, D., Bost, C.-A., Crawford, R.J.M., Crossin, G.T., Cuthbert, R.J., Dann, P., Davis, L.S., De La Puente, S., Ellenberg, U., Lynch, H.J., Mattern, T., Pütz, K., Seddon, P.J., Trivelpiece, W. & Wienecke, B. (2015) Pollution, habitat loss, fishing, and climate change as critical threats to penguins. *Conservation Biology*, **29**, 31–41.
- Trivedi, M.R., Berry, P.M., Morecroft, M.D. & Dawson, T.P. (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Global Change Biology*, **14**, 1089–1103.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Varty, A.K. & Zedler, J.B. (2008) How Waterlogged Microsites Help an Annual Plant Persist Among Salt Marsh Perennials. *Estuaries and Coasts*, **31**, 300–312.
- Verbeek, H. & Storm, C. (2001) Tidal Wetland Restoration in The Netherlands. *Journal of Coastal Research*, **27**, 192–202.
- Wake, D.B. & Vredenburg, V.T. (2008) Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 11466–11473.

- WallisDeVries, M.F. & Van Swaay, C.A.M. (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biology*, **12**, 1620–1626.
- Wanger, T.C., Saro, A., Iskandar, D.T., Brook, B.W., Sodhi, N.S., Clough, Y. & Tscharntke, T. (2009) Conservation value of cacao agroforestry for amphibians and reptiles in South-East Asia: combining correlative models with follow-up field experiments. *Journal of Applied Ecology*, **46**, 823–832.
- Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B., Roy, D.B., Telfer, M.G., Jeffcoate, S., Harding, P., Jeffcoate, G., Willis, S.G., Greatorex-Davies, J.N., Moss, D. & Thomas, C.D. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.
- Webb, C.E., Oliver, I. & Pik, A.J. (2000) Does Coastal Fore-dune Stabilization with *Ammophila arenaria* Restore Plant and Arthropod Communities in Southeastern Australia? *Restoration Ecology*, **8**, 283–288.
- Weiss, S.B., Murphy, D.D. & White, R.R. (1988) Sun, Slope, and Butterflies: Topographic Determinants of Habitat Quality for *Euphydryas editha*. *Ecology*, **69**, 1486–1496.
- Whitledge, G.W., Rabeni, C.F., Annis, G. & Sowa, S.P. (2006) Riparian Shading and Groundwater Enhance Growth Potential for Smallmouth Bass in Ozark Streams. *Ecological Applications*, **16**, 1461–1473.
- Wilkinson, M.E., Quinn, P.F. & Welton, P. (2010) Runoff management during the September 2008 floods in the Belford catchment, Northumberland. *Journal of Flood Risk Management*, **3**, 285–295.

- Willems, J.H., Peet, R.K. & Bik, L. (1993) Changes in chalk-grassland structure and species richness resulting from selective nutrient additions. *Journal of Vegetation Science*, **4**, 203–212.
- Wolters, M., Garbutt, A., Bekker, R.M., Bakker, J.P. & Carey, P.D. (2008) Restoration of salt-marsh vegetation in relation to site suitability, species pool and dispersal traits. *Journal of Applied Ecology*, **45**, 904–912.
- Woodell, S.R.J. & Dale, A. (1993) *Armeria maritima* (Mill.) Willd. (*Statice armeria* L; *S. maritima* Mill.). *Journal of Ecology*, **81**, 573–588.
- Van der Woude, B.J., Pegtel, D.M. & Bakker, J.P. (1994) Nutrient limitation after long-term nitrogen fertilizer application in cut grasslands. *Journal of Applied Ecology*, **31**, 405–412.
- Young, J., Watt, A., Nowicki, P., Alard, D., Clitherow, J., Henle, K., Johnson, R., Laczko, E., McCracken, D., Matouch, S., Niemela, J. & Richards, C. (2005) Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. *Biodiversity and Conservation*, **14**, 1641–1661.
- Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G., McGlinn, D.J., O'Meara, B.C., Moles, A.T., Reich, P.B., Royer, D.L., Soltis, D.E., Stevens, P.F., Westoby, M., Wright, I.J., Aarssen, L., Bertin, R.I., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J., Soltis, P.S., Swenson, N.G., Warman, L. & Beaulieu, J.M. (2014) Corrigendum: Three keys to the radiation of angiosperms into freezing environments. *Nature*, **514**, 394–394.
- Zedler, J.B., Callaway, J.C. & Sullivan, G. (2001) Declining Biodiversity: Why

Species Matter and How Their Functions Might Be Restored in Californian Tidal Marshes. *BioScience*, **51**, 1005–1017.